DOCTOR OF PHILOSOPHY

Development and Implementation of a New National Warning System for Potato Late Blight in Great Britain

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Development and Implementation of a New National Warning System for Potato Late Blight in Great Britain

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DECLARATION

The results presented here are of investigation conducted by myself. Work other than my own is clearly stated with references to relevant researchers and their publications. I declare that the work presented here is my own and has not been submitted in any form for any degree at this or other university.

Siobhán Roísín Dancey

We certify that Siobhán Roísín Dancey has fulfilled the relevant Ordinance and Regulation of the University Court and is qualified to submit this thesis for the degree of Doctor of Philosophy.

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SUMMARY

Phytophthora infestans (Mont) De Bary, the cause of potato late blight, is arguably the most important species of the genus *Phytophthora* in terms of economic losses and the cost of fungicides used for its control. The Smith Period is a set of temperature and humidity criteria that comprise the national warning system for late blight in Great Britain and is used by the potato industry to aid in appropriate scheduling of fungicide treatments. It was developed in the 1950's and has not been reviewed or modified since its inception. In that time, there has been a change in British weather conditions and a change in the diversity and aggressiveness of the pathogen population. The performance of the Smith Period was examined using a back-testing analysis with a historical national-scale, longitudinal outbreak dataset and corresponding weather data. ROC analysis revealed significant regional variation in the ability of the Smith Period to forecast outbreaks. A series of controlled environment experiments were performed to refine the temperature and humidity criteria that define risk of infection, using isolates of *P. infestans* representative of the contemporary pathogen population in Great Britain. The results showed significant levels of infection under drier (less humid) conditions than prescribed by the Smith Period. These findings were used to develop candidate replacement models for the Smith Period. These were tested for their ability to forecast late blight outbreaks using the same back-testing analysis framework as for the Smith Period. The best prediction outcome was a model that requires two consecutive days with a minimum temperature of 10°C and at least 6 hours each day with a relative humidity ≥90%. This model was named the 'Hutton Criteria,' and was launched by the Agricultural and Horticultural Development Board Potatoes division as the new national warning system for late blight in GB in 2017.

1 CHAPTER ONE: FOUNDATIONS - AN OVERVIEW OF POTATO AGRICULTURE, *PHYTOPHTHORA INFESTANS* BIOLOGY AND POTATO LATE BLIGHT MANAGEMENT

1.1 ABSTRACT

Potato, *Solanum tuberosum*, is one of the most important and widely grown food crops both in Great Britain and around the world. Potato late blight (PLB), caused by the oomycete *Phytophthora infestans,* can rapidly destroy an entire crop and is consistently, each year, one of the biggest threats potato growers face. In this chapter we provide an overview of potato cropping, *Phytophthora infestans* biology and potato late blight disease management, with a focus on decision support, both historically in Great Britain and around the world. Decision support systems (DSS) for potato late bight, derived from scientifically developed and tested models, can provide growers data that can be used to identify high risk periods for infection, growth rates, sporulation risk, spatial spread of disease and recommend fungicide sprays. DSSs aid in the management of potato late blight each year, enabling growers to better understand the disease risk in their field and specifically tailor their fungicide spray schedules and general crop management practices. We highlight the large pool of knowledge available for host, pathogen and environment factors and the different criteria and strategies already in place for disease management. This evaluation will be used as a foundation to guide the development of new models to aid in late bight management in Great Britain.

1.2 INTRODUCTION

Potatoes are important both economically and as a staple food crop, with global production reaching 3.8 million tonnes in 2016 (FAOSTAT, 2017). Potato late blight (PLB), caused by the oomycete pathogen *Phytophthora infestans*, is a major threat for potato growers every year as it can rapidly decimate an entire potato crop with estimated costs of disease protection at £1 billion a year in Europe (Haverkort et al., 2008).

To fully understand the complexity of managing potato late blight a foundation of knowledge regarding the triad of environment, crop and pathogen factors and their subsequent interactions is required (Figure 1.1).

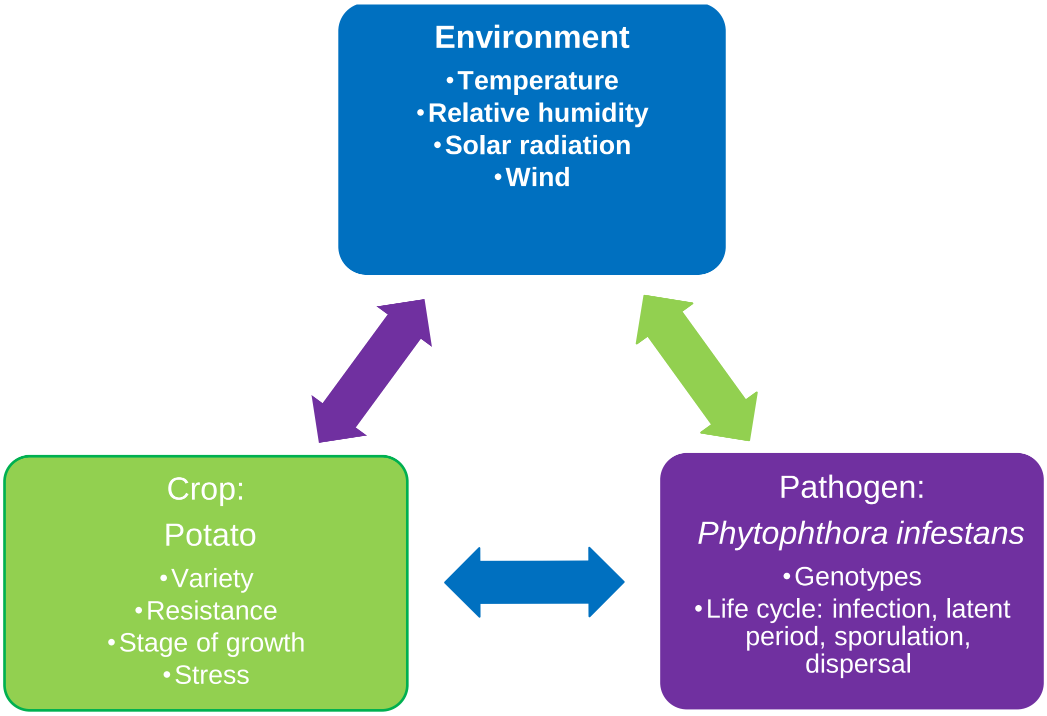

Figure 1.1: Triad of crop environment and pathogen and elements of each which interact to impact on agricultural management practices.

I review here the key points regarding the crop: the potato, the pathogen: *P. infestans* and the environment; focusing on the importance of temperature and relative humidity. In addition, I briefly summarise the strategies currently employed for disease management; from those involving good cropping techniques, breeding, genetic engineering and finally an in-depth look at decision support systems and the criteria involved in them. The overall purpose of this project is to develop models of *P. infestans* infection to support better decision-making with late blight management in Great Britain.

1.3 Potatoes

The potato (*Solanum tuberosum*), has played a pivotal role in the history of human civilization; one could argue that this crop has helped to shape the world we know today in terms of culture, economy and scientific knowledge (Salaman & Redcliffe, 2010).

The potato is a member of the large Solanaceae family of plants including a variety of other important food and horticultural crops such as *Capsicum annuum*, *Datura stramonium* and *Petunia axillaris*. The Solanum genus is the largest branch within the Solanaceae family and contains the potato (*S. tuberosum*) and other important food crops such as the tomato (*Solanum lycopersicum*) and eggplant (*Solanum melongena*).

1.3.1 *Solanum tuberosum*: Early history

S. tuberosum originated in South America and there is evidence of it being domesticated and used by native populations as early as 7000 years' ago (Hawkes, 1990). The *Solanum brevicaule* complex is a group of twenty or so morphologically similar tuber producing plants that have various ploidy levels. They are found in northern Peru, Argentina and southern Bolivia, and are thought to be the ancestors of modern S*. tuberosum* varieties. It has now been shown through amplified fragment length polymorphism (AFLP) analysis, that the domestication of *S. tuberosum* was via a single event within one of the *S. brevicaule* complexes found in northern Peru (Spooner, et al., 2005).

Explorers from Europe to South America during the mid to late 16th century documented the use of the potato by the native populations and it was one of these explorers who inevitably returned with the first potatoes for cultivation in European soils. The first introductions were thought to be in Spain around 1570 and England around 1590 (Hawkes, 1990).

1.3.2 *Solanum tuberosum*: A crop of modern importance

The use of potato as a food crop spread across Europe and the rest of the world and with the advent of industrial agriculture has continued to feature as a staple crop globally. This is evidenced by looking at the Food and Agriculture Organization of the United Nations (FAOSTAT, 2017) figures for 2012; the top commodities produced globally in terms of quantity were sugar cane, maize, rice, wheat, milk and potato, ranking 6th (FAOSTAT, 2017); in terms of global commodity value potato ranked 12th (FAOSTAT, 2017). In 2013 the top producing countries were China (96Mt), India (45Mt), the Russian Federation (30Mt) and the Ukraine (22Mt). The countries with the top five highest yielding potato production systems in 2013 were New Zealand, USA, Belgium, The Netherlands and France achieving between 48 - 51 tons/Ha (FAOSTAT, 2017).

1.3.3 *Solanum tuberosum*: An important crop for Great Britain

The United Kingdom though not listed in 2013 as one of the top five highest yielding countries by the FAO has very frequently in the last 10 – 15 years been ranked here (FAOSTAT, 2017). The total production of the UK potato crop will never compete with places as large as China and Russia but the efficiency of the British system for farming potato is evidenced by its high yields.

The growing regions of Great Britain are divided into four sectors, Scotland with 22% of the potato crop (45% of this being seed), 12% in the West Midlands, 53% in Eastern England and Yorkshire and 14% in the remainder of England and Wales (AHDB & PCL 2015). Figures for production and yield fluctuate from year to year due primarily to weather conditions. The average yield for potato is ~45 t/ha; there are ~125 thousand hectares planted across GB each year, producing an overall total of ~5.3 – 6 Mt each year (FAOSTAT, 2017). A direct comparison of yields, production and area harvested in the UK from 1961 to 2016 shows exactly how the potato industry has been changing (Figure 1.2). If we look at a direct comparison between the years 1962 and 2014 as an example, we see that there was a decrease by ~56% in terms of area harvested and the overall production in tonnes fell by ~18%, keeping in mind that production numbers fluctuate from year to year. The discrepancy between decrease in area harvested and production in tonnes is explained by looking at the yield per hectare; where we see an increase of ~180% between 1962 and 2014.

There were over 70 000 registered potato growers in the 1960s, this has reduced greatly to ~2 150 in 2014 (AHDB& PC 2015). Relatively few varieties dominate GB cultivation. Ten varieties (Maris Piper, Markies, Maris Peer, Lady Rosetta, Estima, Melody, Harmony, Marfona, Hermes, and King Edward) made up 47% of the planted area of GB in 2014 with the top variety, Maris Piper, making up 16% of this total (AHDB & PCL 2015).

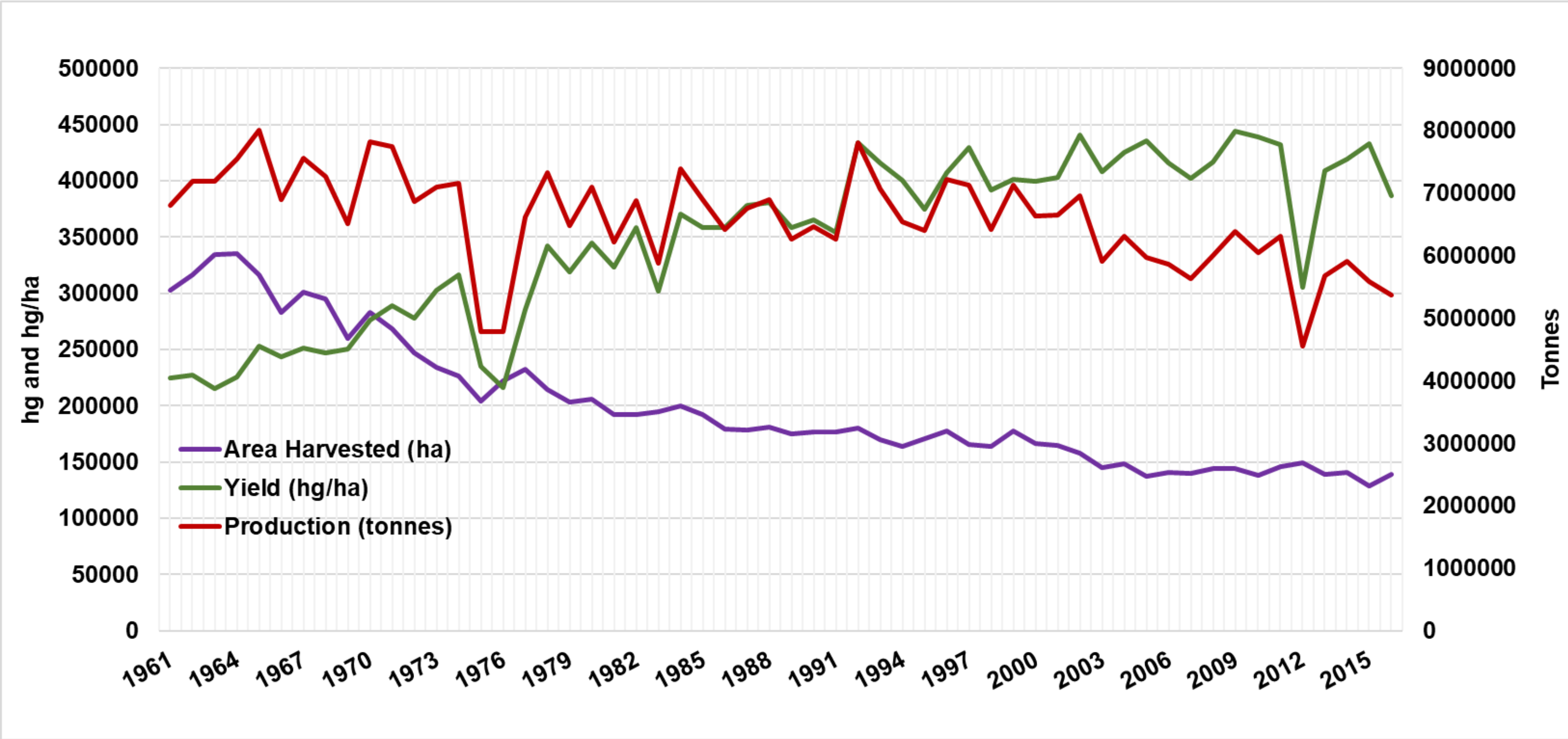

Figure 1.2: Potato production (tonnes), yield(hg/ha) and area harvested (ha) for Great Britain from 1961 – 2016. (FAOSTAT, 2017)

The economics of the potato market can be very volatile for the grower. The price is determined greatly on the success of a growing year; a healthy growing year can over saturate the market and drive prices down. There is also a great deal of interaction with European and global markets; a poor season in another heavily potato reliant country drives prices up in our market because of a higher need to export crops. This means that for the grower, the economic returns from a potato crop are not certain from year to year and as in any form of agriculture there are economic investments made into each crop to get it from field to market and a farmer, of course, wishes to see a financial return above and beyond their input.

1.4 PHYTOPHTHORA INFESTANS

Solanum tuberosum is a host for many pests and pathogens such as: *Alternaria solani* (the causal agent of potato early blight), potato cyst nematodes and perhaps arguably the most devastating and the focus of this research, *Phytophthora infestans*, causal agent of potato late blight. *P. infestans* is an oomycete pathogen which is highly aggressive and can destroy an entire potato crop within a week. It is endemic to central Mexico (Reddick & Mills, 1939, Goss et al., 2014), different to the site of domestication of potato in South America. The first clues as to the centre of *P. infestans* origins were that both mating types of the pathogen are found in central Mexico and the local varieties of Solanum showed resistance to the disease (Reddick & Mills, 1939). Confirmation came from detailed phylogeographic and approximate Bayesian computational analysis (Goss et al., 2014).

1.4.1 ***Phytophthora infestans* and its historical impact**

Perhaps the most well- known and significant impact of *P. infestans* is during that of the Irish potato famine of 1845 – 1850. At the start of this famine, for many social and political reasons Ireland was in a position where about two fifths of the population were reliant solely on potato as their main source of carbohydrate (Grádá,1993). The potato late blight pathogen spread across the whole of Europe at this time but because of the reliance in Ireland on a single crop the impact was extremely drastic; approximately 1 million people died and 1.5 million more emigrated (Gráda, 2000). The impact of this horrific event shaped Irish and global history as the Irish people dispersed and settled internationally.

Scientifically, the Irish potato famine saw the development of our understanding of plant diseases. Away from the tragedy of the starving people of Ireland, debates occurred about the cause of late blight, the famine had demonstrated the consequences of disease epidemics on food crops, creating a desire for better management practices. Originally, the theory of spontaneous generation of disease existed but this was challenged leading to the Paris Academy of Sciences in 1856 offering the Grand Prize of Science to the best response explaining how parasitic spores form, germinate and infect (Matta, 2010). In 1861, Anton de Bary confirmed, with experimental evidence that it was indeed a fungus (now oomycete) which was responsible for the development of the late blight disease and that it did not spontaneously develop because of overwatering (Matta, 2010). This is seen by many as the birth of plant pathology and the beginning of a completely new way to think about plant diseases, their causal agents and thus an ability to manage them.

1.4.2 Phytophthora infestans life cycle

P. infestans has two mating types, A1 and A2, which have the capacity to reproduce both sexually and asexually; both mating types must be present for sexual reproduction to occur. In sexual reproduction, the antheridium (male) and oogonium (female) will fuse leading to sexual recombination and the formation of an oospore. Oospores are also very durable; they have been shown to be able to survive in sandy and clay soils for periods of 34 – 48 months after formation (Turkensteen, Flier, Wanningen & Mulder, 2000). The asexual process involves the formation of clonal sporangium from sporulating hyphae which have penetrated and infected the host plant tissue. The sporangium which are produced from sexual and asexual reproduction methods can infect host plant tissue either through direct or indirect germination methods. Direct germination is more common in warmer temperatures, ~20°C, and involves the sporangia forming a germ tube which directly penetrates the host plant tissue and begins to utilize the plants nutrients to grow and develop hyphae (Elsner, Vandermolen, Horton & Bowen, 1970). In-direct germination occurs in cooler conditions, (~12°C) and the sporangia release biflagellated zoospores which swim in moist conditions until they reach an optimal point for host tissue infection and then begin their disease cycle (Elsner et al., 1970).

P. infestans is hemibiotrophic; having two phases to its infection cycle in a host plant. Initially, there is the biotrophic phase, this is immediately after infection and at the advancing front of the developing lesion when plant defences are suppressed, and the pathogen grows, undetectable to the naked eye utilizing the plant resources. The second phase of infection is necrotrophic; when the disease symptoms becomes visible with the presence of dark wet looking lesions that grow radially (Lee & Rose, 2010). These lesions will eventually produce sporangia, which signals the completion of one disease cycle and the beginning of another. The time from infection to spore production is called the latent period. Late blight is a polycyclic disease, meaning this disease cycle will be repeated many times each growing season; drastically amplifying disease pressure within each year if the environmental factors are conducive.

1.4.3 Phytophthora infestans, a present-day problem

Potato late blight remains one of the most destructive diseases affecting potato crops. The generation time from infection to generation of new spores can occur in as little as two days and, as the disease is polycyclic, the spores produced from each lesion can disperse and infect the tubers of the infected plant, neighbouring plants and fields causing rapid spread of the disease. The disease can cause the destruction of all above ground parts of a plant. If this occurs early in the season the loss of foliage means that the plant will no longer have the capability to photosynthesize and gain the energy required to grow tubers of sufficient size and quantity; this has a very serious economic impact for the farmer. Across the EU the cost of late blight control and losses each year is estimated at around 1 billion pounds (Haverkort et al., 2008).

1.4.4 Phytophthora infestans genome sequence

In 2009 the genome of *P. infestans* strain T30-4 was sequenced using a whole genome shotgun approach, it proved to be a large genome at 240Mb and 74% of the genome was made up of repetitive DNA (Haas et al.,2009). In these gene sparse and repeat rich regions of the genome many effector protein sequences were found, particularly of the cytoplasmic effector families of the RXLR and crinkler proteins (Haas et al., 2009). Effector proteins are crucial in the well documented 'zig-zag' model of plant pathogen interactions (Jones & Dangle.,2006). In this model, effector proteins produced by the pathogen when invading a host cell can develop methods to bypass the pathogen triggered immunity that normally allows the plant to evade disease allowing the pathogen to infect, grow and sporulate. The great diversity of these effectors found in the *P. infestans* genome and their presence in repeat rich regions, where recombination is more likely, allows this pathogen to adapt to different host resistances and environmental stresses and thus remain a real threat to growers.

Considerable genetic diversity exists in *P. infestans* populations in Central Mexico, their centre of origin (Reddick & Mills, 1939, Goss et al., 2014). When the pathogen first migrated to Europe it was likely only in a few samples, and thus diversity of the populations outside of the centre of origin were very restricted. Herbarium samples containing *P. infestans* collected in Europe and Canada from 1845 – 1896 were analysed using molecular markers and indicated that the historic potato famine may have only been caused by a single genotype of blight identified as Herb-1 (Yoshida et al., 2013). Only the A1 mating type was detected across Europe until the early 1980s. It is thought that there was a migration event from central Mexico in the mid-1970s which led to the introduction of new A1 and A2 mating types (Andrivon, 1996, Day & Shattock 1997, Dyer, Matursalt, Drenth, Cohen & Spelman, 1993, Fry & Smith, 1999). The presence of both the A1 and A2 genotypes in Europe means that sexual recombination can occur leading to new genotypes which can potentially be more aggressive and/or fitter than previous genotypes (Li et al., 2012, Cooke et al., 2012). Examples of the changes are the presence of genotypes showing resistance to metalaxyl, a previously important systemic fungicide (Day et al., 2004, Cooke et al., 2012), and more recently a reduced sensitivity to fluazinam (Schepers, 2017). Populations of *P.*

infestans have been tracked with a range of increasingly sensitive phenotypic and genotypic markers originally including mating type, mitochondrial RFLP markers and isozymes (reviewed in Cooke and Lees, 2004). Currently simple sequence repeat markers (Li et al., 2013) are used extensively and collectively all this data indicate that European populations are diverse and in a constant state of flux.

1.4.5 Phytophthora infestans populations in Great Britain

Fight Against Blight (FAB) is a potato late blight monitoring service in Great Britain (GB) which has been operated and funded by the Agricultural and Horticultural Development Board Potatoes (AHDB) since 2003. Blight scouts, farmers and agronomists who are regularly in potato fields, sample infected plant material and record outbreak details such as the variety of potato, the stage of the outbreak and the postcode district it was sampled from. The sample is then genotyped, and the sample details processed at the James Hutton Institute in Dundee, Scotland. This has resulted in a comprehensive data set that has allowed for a very clear picture of the genotypic population of *P. infestans* in GB since 2003 and how the population has changed with time (Figure 1.3).

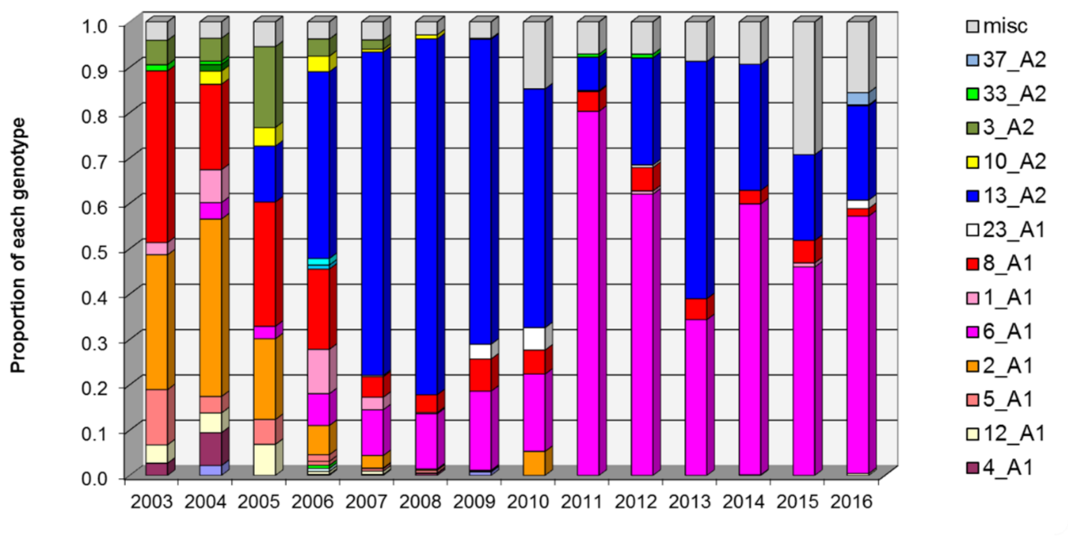

Figure 1.3 Genotypic frequencies of *Phytophthora infestans* isolates sampled from potato late blight outbreaks in Great Britain from 2003 – 2016 by Fight Against Blight (Sourced from D.E.L. Cooke, James Hutton Institute, 2017)

The FAB campaign has documented very clearly the initial emergence and subsequent dominance of the 6_A1 and 13_A2 genotypes in GB (Figure 1.3). These two genotypes, each of a different mating type, are illustrative of how dynamic the populations of blight are in GB. Previous research (Cooke et al., 2012, Chapman, 2012) and communications from growers indicate that these two genotypes are more aggressive than those they displaced, thus explaining their emergence and rapid dominance. Some other genotypes, such as 8_A1 are not as dominant but show persistence in each year of FAB monitoring and dominance in neighbouring Ireland (Cooke, 2015). Finally, the oospore populations in GB appear consistently each year in the FAB data, found mostly in north east Scotland, they have not been a confirmed source of any new dominant genotype.

1.5 LATE BLIGHT MANAGEMENT

The threat of a late blight epidemic is a very serious concern for growers. If they do not make a substantial investment of money, time and care into late blight management each year there is a real threat of losing an entire potato crop with the subsequent financial impact that it will bring.

1.5.1 Disease management practices

A key aspect of disease management is the effective management of *P. infestans* inoculum sources. Of the many practices the most important is the proper disposal each year of refuse piles of potatoes. Refuse piles provide sources of inoculum that overwinter and sporulate on the new growth early in the spring. This can spread and infect not only the growers' own fields but neighbouring fields as spore dispersal on a windy day can be far reaching (Skelsey et al., 2009). Their effective management by herbicides or black plastic coverings would greatly reduce and/or delay initial blight outbreaks each year. It is also critical that growers ensure that all seed potatoes come from a reputable source or that farm saved seed is properly inspected. Crop rotations are an effective way of reducing soil born inoculum load not just for late blight but for other potato pathogens such as potato cyst nematode. The combination of these measures and ensuring that seed potatoes are clean have a great potential to delay the onset of epidemics each year.

1.5.2 Varietal Resistance

The AHDB Potatoes varietal database provides details of important tuber qualities such as bruising and chipping and several relevant disease resistance ratings, including leaf and tuber blight. The resistance ratings are on a scale from 1-9, 1 being highly susceptible and 9 being highly resistant. While there are varieties of potato which show higher resistance to potato late bight, such as Sarpo Mira and Toluca, they may not show resistance to other pathogens or have the desirable qualities that growers require in tubers to ease harvesting or to meet the demands of the market. There is thus no single variety which gives all desirable characteristics and is resistant to all disease. Conventional breeding remains a long and complex process and must continue to respond to a changing pathogen population that alters disease resistance ratings (Lees et al., 2012).

The centre of origin for *P. infestans* was initially suspected to be in central Mexico because the two mating types, A1 and A2 were present in close to equal proportions, but also because the native Solanum species showed natural resistance to *P. infestans* (Reddick & Mills, 1939, Goss et al., 2014). Breeding with the native *Solanum* species led to the identification of a series of resistance genes, or R genes, which can recognize *P. infestans* effectors and confer a level of resistance to the crop (Black, 1960, Malcolmson & Black, 1966). The use of conventional breeding between wild resistant varieties and popular cultivars has been an ongoing challenge since the 1930's; in 1939 Reddick even commented optimistically 'It can be said with some assurance that in the very near future blight immune varieties are likely to be introduced from a number of sources' (Reddick & Mills,1939). However, the use of these resistance genes as a long-term solution has proved problematic as *P. infestans* adapts to and overcomes many resistance genes; relating back to the high number of RXLR and Crinkler sequences found in the genome (Haas et al., 2009).

Breeders have approached more durable sources of resistance by attempting to combine many distinct resistance genes via 'stacking'. In theory, this will take the *P. infestans* populations longer to adapt to and overcome. Such breeding is however painstaking and slow. An alternative approach is to use genetic/cis-genic modification technology to insert the carefully selected set of blight resistance genes into a variety which has desirable characteristics for the consumer and grower (Haverkort et al, 2008). Such approaches have potential, but the use of this technology is still not widely accepted amongst the public creating another set of problems. The classification of gene editing tools like CRISPR/Cas9 (Ran et al., 2013) as genetic modification by the regulatory authorities in Europe is disappointing and limits the potential for rapid progress towards durable blight resistance.

1.5.3 Fungicides

Farmers depend on regular applications of fungicides to manage potato late blight, the spray schedule may be altered throughout the growing season in terms of frequency or type of fungicide based on the environmental conditions, the stage of crop growth or presence of disease. Fungicide active ingredients have different properties often defined as protectants and curatives; protecting a crop before initial infection rather than trying to manage existing infection is the best strategy.

Fungicides can further be classified based on their mode of action as either (1) contact; not taken up by the plant cells and only effective where contact with the plant has been made, (2)translaminar; taken up by the plant cells and moved from the upper parts of the plant to the lower regions and (3) systemic; taken up by the xylem of the plant and redistributed through this pathway.

Fungicide use is regulated to protect the environment, human health and to prevent the build-up of resistance in the pathogen population. Growers must abide by rules such as the spray interval indicated for each fungicide which can range generally from between 7-14 days between sprays or 3-4 uses in total each growing season. As fungicides are an important part of the management of potato late blight, fungicide resistance in *P. infestans* populations is monitored; genotype 13_A2 populations showed metalaxyl resistance in the 2004 (Day et al., 2004, Cooke et al., 2012) and in recent years genotype 37_A2 has been shown to have reduced sensitivity to fluazinam (Schepers, 2017). It is thus important to use fungicides in the most efficient manner possible, to reduce resistance development and to ensure that key products with limited use are available when required as the growing season can last from April to September.

European directives are also driving agriculture to limit pesticide use and reducing the range of products available. Examples include the 'Directive 2009/128/EC of the European Parliament and of the Council of 21 October 2009 Establishing a Framework for Community Action to achieve the Sustainable Use of Pesticides'. A growing public awareness and desire for products which are not heavily treated with pesticides is also an issue. Growers often need to justify every product application as part of their conditions to supply to major potato packers.

1.6 Temperature and Relative Humidity

When determining the risk of infection by *P. infestans*, temperature and relative humidity are critical. The durations and thresholds of these criteria are common features in decision support systems for potato late blight and are observed intuitively by farmers and measured via in-field weather stations and national meteorological networks. Relative humidity is the amount of water vapour present in the air expressed as a percentage of the amount needed for saturation at the same temperature; at 100%RH the air is completely saturated and cannot hold any more water.

There are certain oscillations which occur within a crop field each day between relative humidity and temperature. Each night/early morning period generally sees the highest relative humidity of the day; dew can form at this time on leaf surfaces as they cool by radiating heat, atmospheric moisture condenses at a rate greater than it can evaporate and creates droplets or a thin layer of water (Crowe & Coakley, 1978). Dew thus increases the amount of water vapour present. This is also the time we generally experience the lowest daily temperatures. The lowest point of RH during the day is usually found around noon on dry days. This is the period when temperature and UV are at their highest, causing drying of the leaves and atmosphere. The daily oscillations between temperature and relative humidity are usually smooth and neither generally reach their peak at the same time, not considering rainy days.

The importance of temperature and relative humidity to potato late blight development has been known since it gained focus during the Irish potato famine and it was theorized that the disease spontaneously appeared in wet conditions.

Willard Crosier wrote a seminal and thorough early paper regarding the impact of temperature and humidity on *P. infestans* (Crosier, 1934). He performed an extensive series of experiments using 15 isolates to quantify the impact of the environmental factors temperature and relative humidity on infection efficiencies, growth rates and the formation, longevity and germination of sporangia. Though all isolates used were thought to be of the same genotype, this work provides a snap shot of the characteristics of the pathogen at this period, which can be compared to our more contemporary isolates. Crosier found that when looking at infection on leaves and tubers that sporangia could develop between 3-26°C, noting though that at the lowest temperatures the sporangia were smaller and there were fewer sporangia per sporangiophore. Indirect germination occurred at lower temperature ranges with 9-15°C being ideal. Even at the lower temperature of 6°C he saw 35% germination after five hours exposure, and at 9°C 60% germination after five hours exposure. In terms of his work with relative humidity, he makes a point which is still very relevant; ‘one must never forget that plants adapt to their environment too and that transpiration must be accounted for’. In terms of studying relative humidity in enclosed chambers, a data logger should be used to record the exact environmental conditions; in environments of lower humidity plants can rapidly and drastically change the amount that they are transpiring, thus changing the relative humidity chamber. He found that no sporangia developed below 91% RH and no visible mycelium growth was seen below 85% RH. To illustrate his overall findings, he states that one would expect to find more sporangia at 100% RH and 6°C than at 91% RH and 21°C. In terms of sporangia ability to germinate in lower humidity, he found that at 20°C, for sporangia exposed to 70% RH for one hour only 21.2% germinated, while exposure to 100% RH for one hour led to 80% germination. This indicated that short periods of low RH, or drying conditions, could have drastic effects on infection while short periods of high humidity could be sufficient for a very high level of infection.

There has been a great deal of work from the time of de Bruyn, Reddick and Crosier in temperature and relative humidity research of *P. infestans*. A recent detached leaf analysis of 13_A2 isolates at 13 and 18°C showed that 13_A2 consistently had shorter latent periods and larger lesions than other isolates, and interestingly seemed to be more aggressive at the 13°C temperature point (Cooke, 2012). A continuation of this work (Chapman, 2012) completed a more detailed look at the new dominant genotypes, 13_A2 and 6_A1 in Great Britain. Isolates of 57 contemporary strains of *P. infestans* and their aggressiveness were investigated. Importantly this study demonstrated considerable variation within the same genotypes in terms of incubation period (IP), latent period (LP) and lesion size (LS). Broad conclusions can be drawn from looking at the population as representative as a whole of contemporary genotypes in the UK.

Chapman found with initial characterizations of the isolates on detached leaves that at an ideal temperature of 15°C the incubation period varied from 3 - 4.8 days and the latent periods from 5.5 – 7.7 days. The results found were in-between those results determined by Cooke 2012 for the temperatures of 13 and 18°C. Lowering the temperature slightly with further detached leaf work with a selection of isolates on the temperature gradient plate between 6-20°C, showed that over 90% of isolates infected above 10°C, 84% infected at 8°C and 49% showed signs of infection at 6°C. At 6°C both the 13_A2 and 6_A1 had latent periods below 7 days and at 7 days there were lesions to be scored. Lesions at 6°C were small in comparison to those at higher temperatures, however at 10°C both 13_A2 and 6_A1 were forming large lesions. Isolates of 6_A1 always showed a shorter incubation period than 13_A2 except at the lowest temperature of 6°C. When measuring sporulation, it was found that while lesions could develop and grow from 10°C and below, sporulation in this range was called ‘sporadic’ and non-existent at 5°C and below. The comparison of 13_A2 and 6_A1 at lower temperatures found that 13_A2 was able to infect at a wider range of temperatures, but 6_A1 was more aggressive at the slightly warmer temperatures. The classification of sporulation as ‘sporadic’ at temperatures below 10°C indicates that at these temperatures while disease progresses the conditions are not ideal, and the pathogen is not readily completing its life cycle into the next generation.

Additional investigations of relative humidity were conducted by Chapman with exposures of 100% RH achieved in sealed chambers with moist towels and beakers of water. She exposed whole plants after inoculation in sealed chambers at 100%RH for durations of 0, 1, 2, 4, 6, 8, 10, 14, 18 and 24 hours at 8, 10 and 15°C. In her studies 10, 8, 6, 1 and 0 hours exposure resulted in 93, 85, 35, 4 and 0% infection.

1.6.1 Temperature and Relative Humidity in the field

Each crop has its own microclimate that is affected by factors such as temperature, wind, transpiration, age of crop, aspect and soil moisture to name but a few factors. There are some concerns raised about the use of UK Met Office data for decision support systems when the data comes from weather stations often located at a distance from the crop and at a different height or in very different environments such as air fields. Experimental work generally makes quite precise assessments regarding the impact of temperature and relative humidity on pathogen behaviour and pathogen and host interactions. To apply precise findings to field situations that are broader in scope raises some logical queries. There may be ways to address differences between weather station data and in field conditions such as in, Raposo 1983, while adjusting Blite-Cast to incorporate weather data they adjusted Bayes theorem to correct for the moisture or RH observed in the field and that forecast by the airport weather stations (Raposo, Wilks & Fry, 1983).

Predicting crop microclimates is very complex given their inherent variability. The age of the plants and thus the open or closed canopy plays a large role, exposed soils in a young crop create a warmer temperature in the canopy, while an older closed canopy traps moisture better and high humidity levels will last for longer (Hirst & Stedman., 1960). The complexity of irrigation influence on crop microclimate is another aspect to consider, introducing moisture can clearly cause increases in RH that are not measured by meteorological stations.

1.6.2 Leaf Wetness Models

Temperature and relative humidity are critical to leaf wetness, yet neither define it. The relative humidity and temperature in an environment have a direct effect on how quickly water droplets or films evaporate from the leaf surface. Crosier's experiments examined 'leaf wetness' by looking at infection rates, or growth rates after durations of exposure to high humidity at specified temperatures; at high humidity, the atmosphere around the leaf is saturated with water and the drying of liquid containing the inoculum is slower if at all (Crosier, 1934). Becktell in 2005 examined leaf wetness requirements for *P. infestans* infection on Petunia x hybrida and used humidity tents with plastic sheeting and humidifiers to maintain high levels of humidity, verified with data loggers, and equating the high humidity exposure to leaf wetness. In experimental conditions, high relative humidity can easily be controlled, and leaf wetness tested. One of Becktell's main findings was that most infection occurred within 6 hours of inoculation when kept at a high relative humidity (Becktell, 2005).

Leaf wetness can thus be estimated or assumed in experimental conditions with controlled environments where plants are exposed to saturated relative humidity. Leaf wetness models which calculate leaf wetness within the field, must be much more complex to incorporate the stage of plant growth, irrigation, shading, solar radiation and wind speed. The complexity this requires was demonstrated by a leaf wetness model constructed by joining and adapting several models which found that one must have the following data; above canopy wind speed, air temperature, relative humidity, net radiation and within canopy temperature (Jacobs, Heusinkveld & Kessel, 2005). Further to this, the temperature and relative humidity measurements within a canopy may vary greatly within a single field for a multitude of reasons such as aspect, shading and soil structure.

Leaf wetness duration sensors are tools that are utilised to capture in field data and produce leaf wetness duration readings. One major problem with them is that there is no standardized method for calculating leaf wetness duration as there is with other criteria such as temperature and relative humidity and the sensors generally require on-site calibration (Rowlandson et al., 2015). Efforts to standardize a leaf wetness measurement for in field are ongoing (Rowlandson et al., 2015). Empirical models aim to avoid the leaf wetness sensor problem with calculations of the more reliable and standardized variables such as temperature, relative humidity and precipitation. Bregaglio, 2011 compared six different leaf wetness models and was able to identify a classification and regression tree leaf wetness (CART) model as preforming best (Bregaglio, Donatelli, Confalonieri, Acutis & Orlandini, 2011). This study also identified some other factors of interest such as, the use of hourly data compared with daily data lead to the decrease in model performance, highlighting the importance of precise data when calculating leaf wetness (Bregaglio et al., 2011). The CART model and a fuzzy logic model were tested in their ability to determine leaf wetness durations in a forecasted manner and thus be able to input the data into decision support tools (Kim & Gleason, 2005).

1.7 DECISION SUPPORT SYSTEM REVIEW

Decision support systems (DSS) for potato late blight are aids which use scientific models along with environmental, crop and pathogen information to quantify disease risk so that growers can make a more informed decision in the management strategy for their crop (Forbes 2004, Mackerron & Haverkort, 2004, Cooke et al., 2011). The development of credible and reliable aids is from a combination of historic analysis, experimental investigation and trial runs of systems to develop, test and validate theories prior to recommendation of use to growers. The wrong decision by a grower in terms of disease management can be detrimental, so often a DSS is a guide and will not be solely relied upon. Unreliable DSSs will have a negative impact and quickly damage the reputation of the DSS provider, it is therefore vital that the DSS models are reliable and validated.

1.7.1 The Smith Period

The first set of ‘rules’ in Europe for conditions conducive to late blight development were from the Netherlands in 1926 (Van Everdingen, 1926). Weather prior to late blight outbreaks from 1919 – 1923 were recorded and used to define four rules of weather criteria, which occur two weeks before a late blight outbreak:

(1) 4 hours of dew during the night
(2) Minimum night temperature of ≥10°C
(3) Mean cloudiness on the following day not below 8-10
(4) Measurable rainfall not below 0.1mm in the 24 hours following the dew night (Bourke, 1955)

With this system as a baseline, an 11-year study of meteorological data from the Seale-Hayne agricultural college in Devon, England and the corresponding potato late blight outbreaks were used to define a set of risk criteria for Great Britain. They were called the Beaumont criteria and were defined as two consecutive days where:

(1) Minimum temperature ≥10°C
(2) Relative humidity >75% (Beaumont, 1947)

Beaumont's criteria were meant to trigger alerts to growers based on flushes of warnings within the growing area indicating high risk for disease development. They were further tested for Scottish regions from 1944 – 1948 and found that they predicted blight outbreaks after the end of June (Grainger, 1949). This introduced the idea of a 'zero date' for risk criteria; early season outbreaks could not reliably be predicted with the criteria but after the zero date in the growing season they could be used.

The Smith Period was a refinement of the Beaumont Criteria in the 1950's, defined as, two consecutive days where;

(1) The minimum temperature ≥10°C
(2) On each day there are at least 11 hours where the relative humidity is ≥ 90% (Smith, 1956(b))

Smith also added a near miss category to his criteria: when on one of the two consecutive days there were ten hours rather than eleven where the relative humidity was ≥ 90% and eight for locations on the lee of hills. When examining monthly relative humidity totals across England, Smith found there were clear drops in the number of hours for those areas in the lee of hills, or the 'dry side' (Smith, 1956(b)). Smith compared his new criteria to the

Beaumont criteria using single weather station data and outbreak data from 1950 – 1954; focusing on 43 of 220 outbreaks during this period which had not received Beaumont criteria alerts. The new Smith Periods predicted 29 of the 42 missed outbreaks.

1.7.1.1 Blightwatch

Smith Period alerts are provided freely by the Agricultural and Horticultural Development Board, Potato Division (AHDB Potatoes) through a system called Blightwatch in Great Britain; email or text message alerts are sent to the grower if a Smith Period occurs in their specified postcode district. The alerts are calculated using a network of UK Met Office synoptic weather stations across the country which have been interpolated to postcode districts. The Blightwatch website (https://blightwatch.co.uk/) also allows the grower to access calendar data of alert occurrence, minimum temperature and durations of high relative humidity throughout the growing season for the postcode districts of interest to them.

1.7.1.2 BlightCast

BlightCast is an online tool run by Syngenta which provides risk alerts for potato late blight to growers as well as information on when to apply fungicides in the United Kingdom (www.syngenta.co.uk/blightcast). Previously they provided alerts based on the Smith Period. In 2015 they released a new set of risk criteria where the minimum temperature of the Smith Period was reduced to 8°C. This was to reflect recent research (Cooke et al., 2012) and growers opinions that the contemporary genotypes of *P. infestans* in Great Britain were able to infect at lower temperatures.

1.7.2 Decision Support Systems Abroad

There are a variety of different kinds of decision support system for potato late blight which are briefly compared. They have been broken down into four main categories, (1) yes/no risk-based criteria, (2) negative prognosis models, (3) gradient-based systems and (4) combinations, which are composed of multiple systems. The development of DSSs is ongoing, but older systems such as the Smith Period are still relevant and are often adjusted over time rather than replaced completely.

1.7.2.1 Yes/No Risk Criteria

Yes/no criteria are the simplest form of DSS for potato late blight and they are often incorporated into combination systems. There are five basic systems identified which have temperature and relative humidity criteria thresholds which must be met for specified durations of time to indicate risk and may include a leaf wetness or precipitation parameter (Table 1.1). They range in dates of development from the 1950's to the 1990's. Only one has a minimum temperature criterion below 10°C and two have a RH threshold below 90%.

Table 1.1: Temperature, relative humidity, leaf wetness and duration criteria for identification of high risk environmental conditions for potato late blight infection from five different decision support systems

System	Country	Year	Temp.	RH	Leaf Wetness/ Precipitation	Duration
Smith Period[1] (infection)	Great Britain	1950	Minimum ≥10°C	≥90% for 11 hours		Two consecutive days
Irish Rules[2] (infection)	Ireland	1953	≥10°C	≥90%	4 hours	1. Twelve hours with leaf wetness 2. 16 hours without leaf wetness
Førsund rules[3] (infection)	Norway	1965	Max 17 - 24°C Min ≥ 10°C	≥75% at 00:00	≥0.1mm	One Day
Førsund rules – Televis (infection)[4]	Norway	1995	Max 16(15) - 24°C Min ≥ 8°C	≥75% at 00:00	≥0.1mm	One day
M.I.S.P. (sporulation)[5]	Switzerland	1990	≥10°C	≥90% for 6 hours	6 hours precipitation	One day

(1) Smith, 1956. (2) Bourke, 1955. (3) Førsund, 1983. (4) Hermansen & Amundsen, 1997 (5) Bugiani, Cavanni & Ponti, 1993

1.7.2.2 Irish Rules – 1953 - Ireland

The Irish rules (Table 1.1) were developed in the 1950's; this was the same time period during which the Smith Period was developed for Great Britain. Smith employed a historical analysis for development, whereas the Irish rules were developed by Austin Bourke interpreting the experimental results of Willard Crosier from 1934; fundamental versus empirical approaches. The Irish Rules are meant to indicate risk using their criteria in a yes/no fashion, but that risk is accumulated in what are termed 'effective blight hours' to give magnitude to the alerts, every alert period separated by at least five days from another is considered a generation of disease, and alerts are issued after 3 -5 generations of disease (Bourke, 1955). They also employ a zero date, a date before which it is considered difficult to identify blight risk; this was usually considered around mid-June. Met Éireann (the meteorological office in Ireland), are responsible for issuing alerts to growers using observed and forecasted data from synoptic weather stations.

1.7.2.3 Televis – 1990 – Norway

In Norway, the Førsund rules developed in the 1960s (Førsund, 1983) are still used today by the Televis DSS, after only slight modification in 1995 (Table 1.1) (Hermansen & Amundsen, 1996). The modification lowered the minimum temperature threshold from 10°C to 8°C as potatoes are grown in northern regions in Norway where they frequently experience low temperatures that they find to be a key limiting factor for blight development. It has been noted that the use of precipitation as a criterion has caused periods of high humidity and dew which are conducive to risk to not be alerted as there was no actual precipitation. There are on average 0 – 7 fungicide sprays a year and this has been found to be reduced to 0 -3 with the use of the guidance from Televis system (Hermansen & Amundsen, 1996).

1.7.2.4 VNIIF Blight – 1990 - Russia

The Russian DSS for potato late blight was developed at the All Russian Research Institute of Phytopathology (Filippov et al., 2009). It is freely accessible through an online calculator which simply asks you to look up the minimum and maximum temperatures forecasted for the next five days as well as whether or not rain is forecast, and this will then calculate a risk factor. The risk factor is a statement saying whether the conditions are favourable and a numerical value quantifying the risk. Behind this simple calculator is a mathematical model calculating risk determined from field trial data.

1.7.2.5 M.I.S.P. – 1990 – Italy

Main infection sporulation period (M.I.S.P.) was developed in Switzerland and is designed not to identify periods of high risk for infection but periods of high risk for sporangia release (Table 1.1). These criteria for spore release have been validated using sporangia capture in the field and it was found that the highest number of sporangia were found 1-2 days after M.I.S.P. criteria and that only one out of 14 predictions did not see increased level of disease in untreated crop after (Ruckstuhl, Cao & Forrer, 1998).

1.7.2.6 Negative Prognosis Models

Negative prognosis models do not indicate risk of disease but provide scores on when the environmental conditions are not conducive to disease and thus outbreaks would be unlikely. They are systems which are commonly used to detect the first outbreaks in the growing season.

1.7.2.7 Negative Prognosis Model – 1966 - Ullrich and Schrodter's

Ullrich & Schrodter's negative prognosis model relies on recording tabulated measurements of temperature, relative humidity and precipitation data being monitored daily (Ullrich & Schrödter, 1966). Each day the range of temperature and relative humidity levels are scored in their calculation table, from which each day is assigned a value. The values are multiplied by the corresponding multiplication factor and summed for each week. The first spray warning of the year, if the previous year was a heavy year for blight, is triggered by a summed value of ≥150, which indicates disease incidence of 0.1%. If the previous year was a light blight year, then the summed value required to trigger a first occurrence is increased to ≥250, indicating disease incidence of 1%. Further spray warnings are triggered after a summed value of ≥150. There is no option to record temperatures below 10°C on the table, so this appears to be the minimum temperature threshold and all relative humidity calculations rely on it being ≥90% for durations of either 4 or 10 hours, unless there is precipitation.

1.7.2.8 I.P.I – 1990 - Italy

Indice Potenziale Infettina (I.P.I) is a negative prognosis model for identifying the first outbreaks in a season in Italy. It has been in use since the 1990's; providing data on disease occurrence and first spray advice. It requires daily average, minimum and maximum temperatures, average relative humidity and amount of rainfall (Bugiani, Govoni, Cobelli & Rossi, 1998). The minimum values from which it begins to score are temperatures ≥ 7°C, rainfall > 0.2mm and relative humidities ≥79%. There are 4 synoptic met stations in the region of Italy where it is utilized that can be used in forecasting and five meteorological stations with precipitation monitored by overhead radar. Synoptic stations are near airports and the coast, but the other meteorological stations are placed in important agricultural regions providing a combination of weather data. These data are entered into a series of models relating to the biology of *P. infestans* which produces a daily risk value. Historic data analysis found that it alerted on average ten days prior to the first outbreak of the year, however it was found to function best in low blight risk years and was not as effective in high risk years (Bugiani et all., 1998).

1.7.2.9 Gradient based systems

Gradient based systems are those systems which do not have a defined yes/no threshold which will trigger an alert for risk of infection. They are built upon systems of accumulation of criteria over periods of time. The Irish rules have a cumulative element to their model, but it is of the same criteria repeating, the same as the Smith Period occurring over two consecutive days. While gradient based systems assign different levels of risk to a range of temperature and relative humidity combinations which can build up over time. Like the two negative prognosis models, but indicating periods of high risk for blight development, not those periods which are not.

1.7.2.10 Fry – 1983 – Fungicide Application Model

Fry's model for fungicide application requires three inputs; (1) in-field weather data for hourly temperature, relative humidity and daily rainfall, (2) the host or potato resistance rating as either susceptible, moderately susceptible or moderately resistant and (3) the number of days since a fungicide treatment (Fry, Apple & Bruhn, 1983). It contains two sub-models to calculate a number of 'units' for fungicide and for blight. The fungicide unit calculation integrates the time in days since the last application of fungicide and amount of rainfall in that time and provides an output value from 0 – 8. To calculate the blight 'units', temperature, varietal resistance and number of hours of relative humidity ≥90% are used to calculate a value from 0 -24.

The decision rules then incorporate the data for the potato varietal resistance rating as being susceptible, moderately susceptible or moderately resistant. The model outputs find that susceptible cultivars require shorter periods of RH ≥ 90% for infection, while more resistant cultivars require longer periods as well as higher temperatures (Fry, Apple & Bruhn, 1983).

1.7.2.1 Prophy – 1988 – The Netherlands

The Prophy model was developed in 1988 in the Netherlands, as a set of high risk criteria for disease development. It uses in-field data sensors to calculate risk rather than synoptic weather stations and provides a score each day between 1 -100, based on the risk criteria and the disease pressure from neighbouring outbreaks (Nugteren, 1996).

Further to identifying risk periods for potato late blight development, the Prophy system also provides spray advice considering details such as: the last spray, type, dose rate, wash off, irrigation and potato variety resistance. The first spray of a fungicide in this model is triggered when the crop height reaches 15cm, but this can be extended a further ten days for resistant varieties. Further fungicide sprays are protective for eight days on susceptible varieties; this can be extended 1, 2 or 3 days for more resistant varieties. The period between recommended sprays can be shortened based on crop growth rate and favourable days for blight development or if there is precipitation. The system is also able to incorporate a risk based on blight pressure from neighbouring fields. Comparisons of using Prophy with the standard seven-day spray regime have shown that it reduces the number of fungicide treatments on average by 2.5 which saves the grower €60 per ha (Nugteren, 2004).

1.7.2.2 Guntz Divoux – 1991 - France

Guntz Divoux is a very in-depth qualitative model from France. It calculates three levels of risk for *P. infestans* spores; (1) infection, (2) incubation and (3) sporulation. The level of risk is in two categories called ‘gravities’, these have been calculated based on Bourkes data used in Ireland of the 12 and 16-hour durations of relative humidity ≥ 90% and temperatures ≥10°C, which Bourke in his empirical methods took from Crosier’s findings.

The incubation period of sporangia is calculated from the average daily temperature and an accumulation of specified ‘units’ based on temperature over time starting at either 8 or 10°C (Duvauchelle & Dubois,1996). Similarly, sporulation is calculated through an accumulation of temperature based ‘units’ on a different scale than those used for incubation (Duvauchell & Dubois, 1996).

1.7.2.3 MILSOL - France

MILSOL provides a quantitative assessment in France for infection, incubation and sporulation of *P. infestans*. The calculation for risk in MILSOL depends on a relative humidity requirement; if the relative humidity is below 90% then the value is 0, above 90% there is a model to quantify the number of sporangia which will infect. Following this there are development units with an optimum temperature of 21°C and a calculation for incubation units from which to determine risk. A potential of sporulation is calculated using necrosis of the lesions, as a function of age of the necrosis, ideally with a relative humidity of 100%, and temperature of 21°C.

1.7.2.4 Blite Cast – 1970 - USA

Blite Cast in the U.S.A. is a decision support system composed of two integrated sub models; Hyre and Wallin’s, which are used to model the first possible infection by *P. infestans* in the year. The model requires values for temperature, relative humidity, precipitation and leaf wetness. Like many other DSS's discussed, the underpinning criteria are temperature thresholds when the relative humidity is ≥ 90%. Hyre's criteria calculate for the first occurrence of blight to be 7-14 days after the first accumulation of 10 rain favourable days or with Wallin's criteria 1-2 weeks after 18 severity values.

1.7.2.5 Combination systems

Combination systems are those which have taken some of the previous models mentioned and combined them to create a more powerful alert system.

1.7.2.6 NegFry

NegFry is the combination of two separate DSSs; Ullrich and Schrodter's 1966 negative prognosis model and Fry's 1983 fungicide application model (Fry, Apple & Bruhn, 1983, Ullrich & Schrödter, 1966). The output of the system is two graphs, one for crop susceptibility and one for weather data.

1.7.2.7 PCA – 1993 - Belgium

The Centre for Applied Potato Research (PCA) in Belgium started a warning service for late blight in 1993. PCA provides advice throughout the growing season using the Guntz-Divoux model, originally developed in France but modified for use in Belgium, on when and which fungicide to use. Belgium operates 24-hour automated weather stations across the country which are used to calculate risk from the system. The criteria for risk used in this system are 10.5 hours with RH≥ 90% with no more than a four hour gap in this period when it drops below 90% and if it does so, never below 70% and the average temperature during this period should be no less than 7°C (Minne, 1996). They also operate a 0-4 classification system for risk of infection, 0 is equal to no risk and 4 is the highest. They calculate incubation and sporulation by monitoring the daily temperature and accumulating risk units.

1.7.2.8 Plant Plus – 1994 – The Netherlands

The Dacom System, previously Plant-Plus, is one of the most sophisticated DSSs for potato late blight has been in use since 1994 in the Netherlands, operated by DaCom and accessible online, it requires a minimum investment of €350 per year by the grower (Hadders, 2008). DaCom is a large company servicing more than 26 000 farms (769 000 ha) in more than 50 countries (DaCom). Plant-plus is an integrated system, which means that it is built by combing multiple models, they can be combined to meet the needs of the grower or incorporate new developments in research. It uses hourly weather data both retrospectively and ten days forecasted for temperature, relative humidity, wind direction, speed, solar radiation and precipitation (Hadders, 2008).

There are three main parts to the core Plant-Plus model output, (1) the assessment of the unprotected crop, (2) the disease cycle of *P. infestans* and (3) fungicide treatment recommendations.

The first part of the model, the assessment of the unprotected foliage, is calculated from information provided by the grower on a standard scoring sheet. The system then calculates the growth rate and emergence of new unprotected leaves that will be at risk of infection as they will not have been protected by previous sprays. Meteorological data is also incorporated to determine the loss of protection due to precipitation, degradation from solar radiation and fungicide deterioration.

The second part of the model looks at the disease cycle of *P. infestans* and is further divided into four subsections: (1) spore growth, (2) ejection and dispersal of spores, (3) germination and penetration and (4) incubation. Spore growth is calculated based on relative humidity and the output from this model feeds into the model for ejection and dispersal of spores. The model considers the source of spore inoculum and conditions during inoculum release; spore quantity, wind speed and direction.

The third part of the model calculates risk by multiplying the total number of spores present in a specific hour by the length of time it is determined that they can infect and the amount of unprotected crop. Advice is then provided as to whether a fungicide spray is required and if so which kind of fungicide treatment should be used; contact, translaminar or systemic.

The Plant-Plus model output is two graphs, which summarize the two aspects of the model the amount of unprotected crop and the chance of an infection event; it shows data both retrospectively and forecasted for ten days; allowing growers to take preventative measures. If an event is forecasted or was detected in the previous 12 hours; protective measures are often more cost effective for the grower than the fungicides to treat a past infection event (Hadders, 2008), in dry conditions it is said that the system can confidently give advice not to spray for 11 – 24 days (Wander, Spits & Kessel, 2002).

1.7.2.9 SYMPHYT – 1994 - Germany

SYMPHYT is a two-part DSS which was developed by Zepp and provided by Informations system Integriete Pflanzenproduktion (ISIP) for use in Germany (Kleinhenz, Falke, Kakau & Rossberg, 1998). This model, perhaps due to Germany's size considers analysis of the different climatic districts within the country and provides different assessments for each region. There are also two different 'risk levels' for potato growing regions as well; risk 1 is the high-risk areas close to lakes, water logged soils or farms where highly susceptible varieties are grown, risk two classifies all the other lower risk regions and more resistant potato varieties (Kleinhenz et al.,1998). The two models, SYMPHYT 1 and SYMPHYT 2 work much like the Negfry model with SYMPHYT 1 being used for first outbreaks and SYMPHYT 2 being used later in the season. SYMPHYT 1 requires inputs of temperature and relative humidity every three hours as well as daily precipitation values and is run twice a week using forecasted weather data for up to eight days. A historical validation of this model using 330 outbreaks from 1994 – 1998 showed that 90% of outbreaks received a SYMPHYT 1 alert in the previous 1 -14 days (Kleinhenz et al., 1998). The only test year during the validation for which it did not work efficiently was in 1997 when only 60% of outbreaks were predicted, they related this to the fact that it was an extremely wet year and SIMBLIGHT, another model, was developed to compensate for such situations. SYMPHYT 2 assesses disease pressure after the initial outbreak each year. This model requires hourly temperature, relative humidity and rainfall data as well as crop variety and emergence data. The model calculates a disease progress curve and monitors disease in treated and untreated field plots. Further to monitoring the disease pressure the model also provides a recommendation for fungicide use and spraying schedule. It has been shown to reduce the number of fungicides sprays in a year from 6-7 to 4-5 when compared with conventional strategies but these reductions in use were mainly seen in periods of very dry weather and not during rainy periods.

1.7.2.9.1.1 Untreated Plot Monitoring

In 2000, Zeneca Agro established a network of treated and untreated plots (until the first sign of blight) using the most common potato cultivars across Germany to monitor for the presence of potato late blight throughout the growing season. Disease level is monitored within these crops weekly and used to aid in first detection and intensity of potato late blight each year. The resulting advice from the SYMPHYT systems and the treated and untreated plots were published weekly in an agricultural paper.

1.7.2.10 PhytoPre +2000 – 2000 - Switzerland

PhytoPre +2000 is a DSS developed in Switzerland by the research station Reckevholz-Tanikon. The M.I.S.P. (main infection and sporulation periods) and Ullrich Schrodters negative prognosis model are used with in-field rainfall amounts, local and regional weather data and two day forecasted data from Meteos Swiss. The system requires hourly data for temperature, relative humidity and rainfall. The M.I.S.P. DSS provides daily mapped data for the recent infection and sporulation periods which have occurred using a traffic light system to easily display risk (Steenblock, Forrer & Fried, 2001). Spraying recommendations are also provided based on the growers' specific field conditions, including disease situation, weather and previous spray data. The negative prognosis model calculates the actual infection potential using the pathogen characteristics. It has been adapted to the specific growing regions of Switzerland through a network of 150 unsprayed plots which were monitored, and their disease progress curves were all found to be similar, varying only based on start date, a general logistic curve was then fit to predict the probability of infection.

PhytoPre offers a lot of options to growers in how to best use the system; they can receive in depth information with field specific advice, late blight information, rainfall and fungicide application data, they can opt for weekly bulletins of the late blight occurrences and rainfall data for the whole country or they can receive a risk map with all infection potentials as well as late blight outbreaks. Fungicide advice returns a graph with selected fungicides showing their length of protection, weather conditions permitting. In terms of performance of the system and acceptance by growers, a 2001 questionnaire showed that 80% would continue to use the system and 90% would recommend it.

1.7.2.11 VIPS – 2001 – Norway

VIPS is an online site from which the potato late blight DSS has been operated in Norway since 2001. The system on the VIPS site consists of three elements, (1) monitoring early infections of potato late blight through map data and scouts looking for the first signs of blight, (2) Ulrich & Schrodters negative prognosis model to identify the first spray warning for the year and (3) Førsund rules (Table 1.1).This more modern system provides a web based access point where growers can click on a map of the Norwegian regions and zoom on the areas that are of importance to them to see what warnings have occurred at their networks of over 70 meteorological stations (Folkedal & Brevig, 2004).

1.7.2.12 MILPV – 2004 – France

The French DSS, MILPV is composed of two sub models; Guntz Divoux providing a qualitative risk factor and Milsol providing a quantitative risk factor. MILPV itself is divided into three parts; the core MILPV of the Plant Protection System, which receives the incoming meteorological data, runs the sub models and receives inputs from local farmers and trial sites, the second MILPV, designed for working with researchers and the third MILPV, designed for growers. The MILPV system requires the growers to install software to run the required calculations and record the required crop and weather data, such as variety, fungicide treatments, irrigation, stage of growth and precipitation. The grower will receive environmental alerts from the main MILPV site but needs to input their own crop and local information to receive the best advice regarding sprays.

1.8 Conclusions

Potato has long been a valuable crop both around the world and in Great Britain and as long as the potato has been an important crop so too has *Phytophthora infestans*, causal agent of potato late blight been a serious concern for growers. There is no panacea for potato late blight. Plant pathogen interactions are often described as ‘an arms race’, indicating that this may not be a game that can be won.

Potato late blight can however be managed, and as our knowledge and understanding of the host, pathogen and environment increases so does our ability to develop new strategies for management. We understand the composition of the genotypic population of *P. infestans* in more detail than ever before. We are able to address the presence of new genotypes with resistances to our fungicides, such as 37_A2 and its fluazinam insensitivity, advising growers in the area where this genotype has been detected to be alert.

Due to the importance of potato crops and the serious potential impact from *P. infestans* infection, there has been a great deal of genetic and molecular level research into understanding the host, pathogen and their interactions. There is a wealth of knowledge available and the possibility that perhaps using breeding or genetic engineering techniques we may one day be able to develop a durable resistance to *P. infestans*, so that growers will not have to rely solely on regular fungicide sprays to produce the potato crops demanded by the market and consumer.

The development of scientific models and decision support systems (DSS) for potato late blight creates tools that can be utilised by growers immediately to help manage late blight. We have described many different DSS and used them to set the context for the current studies. There are common threads among them, focusing on temperature and relative humidity criteria to identify periods conducive for infection, quantifying the growth rate of disease and likelihood of disease spread. The more sophisticated DSSs can identify when sporangia are likely to disperse and spread into a crop, what the spore load will be, when periods for infection occur and provide advice to the grower based on resistance of potato cultivar, previous sprays and which future sprays are advised. The more advanced DSSs are more likely to be commercially owned and require an investment from the grower to benefit from the knowledge. The freely accessible systems are often based on simple risk criteria, such as the Smith Period, and while they are simpler they provide alerts for the entire country.

Each country often has specific limiting factors dependent on their geographic location. *P. infestans* populations vary across different countries, with many clonal populations becoming established and adapted to local environments. Norway has one of the only DSSs with a minimum temperature threshold below 10°C, but this reflects their northerly location and the fact that temperature is their limiting factor for disease development (Hermansen & Amundsen, 1996). While DSSs in California often focus at higher temperature range not seen in many northern European DSSs. Each DSS also reflects the climatic nature of the country, many continental regions use one system for the entire country and do not readily report on climatic differences within the country. SYMPHYT in Germany however notes the need for use of defined climatic regions to assess DSSs performance, while I.P.I in Italy takes not of varying conditions between coastal and inland regions.

It is clear that the establishment of a DSS for late blight for each country to reflect the different climatic districts and populations of *P. infestans* has been a common approach historically, however in more recent times there are examples of systems such as DACOM being utilized on an international basis. The utilization of a system designed specifically for a country or for the adoption of another countries system is reliant on the resources of the country, the climatology of the country and the needs of the growers.

2 CHAPTER TWO: HISTORIC DATA ANALYSIS OF SMITH PERIOD PERFORMANCE

2.1 ABSTRACT

The Smith Period is used in Great Britain (GB) as an indicator of risk for potato late blight (PLB) development. It was developed specifically for GB in the 1950's and has not been reviewed or modified to date. In this study we evaluated the performance of the Smith Period as a blight risk indicator using national-scale late blight outbreak data from 2003-2014 (> 2000 outbreaks across GB) and corresponding weather data. Occurrence and frequency of Smith Periods across Great Britain were visualised and related to outbreak distributions using GIS. Receiver operator characteristic (ROC) curve analysis was used to evaluate the ability of the Smith Period to indicate risk prior to reported outbreaks. The Smith Period yielded an area under the ROC curve of 0.686 (95% CI = 0.540-0.832) for the entire outbreak dataset, signifying a 'fair' disease risk forecasting system. When the analyses were repeated using subgroups of data according to the climatic districts of GB, we found significant variation in the performance of the Smith Period across the country.

2.2 INTRODUCTION

Potato late blight (PLB) is a concern for growers each year around the world. The disease, caused by the oomycete *Phytophthora infestans*, spreads rapidly and can destroy an entire crop within weeks. Growers typically take a prophylactic approach towards disease management, from the initial fungicide spray each year they will then continue to spray at regular intervals of seven days with variation dependent on weather conditions, plant growth and disease pressure. Decision support systems (DSS) are available to help growers identify low- and high-risk periods for disease development. These range in complexity for potato late bight (Cooke et al., 2011), from those that identify high risk periods (Bourke, 1955, Førsund, 1983), to those that incorporate previous fungicide sprays and offer detailed spray advice (Fry, Apple & Bruhn, 1983, Hadders, 2008) and even those that contain a spatial element of disease spread (Ruckstuhl, Cao & Forrer,1998). Each country often has a specific DSS for potato late blight that is predominantly used, usually having been developed to meet the needs of that country from localised data often including historic weather data, forecasted data, *P.infestans* genotype data and the location of potato growing regions. Each DSS is a tool in the growers' toolbox designed to enable growers to more confidently, responsibly and effectively establish fungicide spray regimes while reducing unnecessary sprays. The decision support tool most widely and freely available for use in Great Britain (GB) is the Smith Period.

The Smith Period has been used to indicate high risk periods for potato late blight development in GB since it was developed in the 1950's (Smith, 1956(a)). It is a simple set of weather-based rules, defined as two consecutive days each with a minimum temperature ≥10°C and at least 11 hours of relative humidity ≥90%. Smith Period alerts are currently delivered to approximately 14,000 subscribers of the Agricultural and Horticultural Development Board, Potatoes Division (AHDB Potatoes) funded 'Blightwatch Service,' which freely provides daily temperature and relative humidity data at the postcode district level, and alerts via email and text message to growers when a Smith Period occurs in their specified postcode district location (https://blightwatch.co.uk/). The Smith Period was originally developed from the Beaumont criteria (Beaumont, 1947), which was defined as two consecutive days where the minimum temperature is ≥10°C and the relative humidity does not fall below 75%. Smith examined a series of late blight outbreak maps from 1950-1954 and found that 43 out of a total of 220 forecasts of late blight risk made using the Beaumont criteria were not valid for their respective zones. He then analysed the humidity conditions at each of the participating weather stations and modified the relative humidity requirement of the Beaumont criteria from a minimum of 75% over two days, to a total of at least 11 hours of relative humidity ≥90% on each day. This reduced the proportion of invalid forecasts from approximately 20 to 10%.

Although Smith improved on the Beaumont criteria, over 60 years have passed since the performance of this DSS was assessed. This is a concern as GB has seen a change in weather conditions and the introduction of the

A2 mating type of *P. infestans* into the country, leading to change in pathogen diversity and aggressiveness (Spielman et al., 1991, Cooke et al., 2003, Day, Wattier, Shaw & Shattock, 2004, Lees et al., 2012). The objective of this study was to examine the relevance and performance of the Smith Period as a disease risk forecasting system for the contemporary pathogen population under the current climate. A total of 12 years of national-scale, historical weather and outbreak data were explored using ArcGIS, and the performance of the Smith Period evaluated using ROC analysis.

2.3 MATERIALS AND METHODS

2.3.1 Data Sets:

2.3.1.1 *Historical late blight outbreak data*

The 'Fight Against Blight' (FAB) service is funded by AHDB Potatoes and has been recording and sampling potato late blight outbreaks across GB since 2003. When blight scouts observe a PLB outbreak they sample the outbreak and report the following details; (1) the postcode district location of the outbreak, (2) the date of outbreak, (3) the stage of the outbreak (single plant, patch, several patches, scattered and severe), (4) source of disease, (5) the variety of potato and (6) the name of the reporting scout. Samples of infected leaves are sent to the James Hutton Institute in Dundee where they are officially numbered, recorded and genotyped. The locations and dates of the FAB outbreak data from 2003-2014 (> 2 000 outbreaks), were used in this analysis.

2.3.1.2 *Historical weather data*

The weather data used by UK Met Office (UKMO) to calculate Smith Period alerts for the Blightwatch service were used in this study for analysing the performance of the Smith Period. The UKMO synoptic met office stations are located on flat open ground, away from obstructions with equipment 1.25m above ground height. Measurements of daily minimum temperatures and number of hours per day of relative humidity ≥90% from April 1 – September 30 (typical potato growing season), 2003-2014 were provided for 652 different locations across Great Britain. Each of the 652 locations was interpolated by UKMO from their network of weather stations; data was interpolated from a series of stations for each point as UKMO stations can be cycled on and off line throughout the year. GB potato growers receive Smith Period alerts according to their postcode district (>3000 in GB), thereafter UKMO assign each postcode district to the nearest of the 652 weather data points. Thus, each PLB outbreak recorded at postcode-district level, was assigned to a UKMO data point.

2.3.2 Methods:

The historical weather and outbreak data used to examine the performance of the Smith Period were integrated and analysed using a combination of MATLAB for data preparation, data mining and receiver operator characteristic analysis, ArcGIS for spatial analysis and mapping, and GenStat 18th edition for ANOVA analysis.

2.3.2.1 UKMO Climatic Districts

The UKMO has defined nine climatic districts in Great Britain: (1) Scotland north, (2) Scotland west, (3) Scotland east, (4) northwest England and north Wales, (5) northeast England, (6) Midlands (7) southwest England and south Wales (8) southeast England and (9) east Anglia, (Figure 2.1). The climatic districts have definably different (between) or similar (within) climatologies, and these were used to create subgroups of the weather and outbreak data to facilitate an assessment of geoclimatic variation in Smith Period performance. GB postcode districts were aggregated to match UKMO climatic districts by overlaying their respective boundary maps in ArcGIS. UKMO summary data for temperature, sunshine, rainfall and frost in each climatic region were used to characterise overall conditions for late blight across GB during each year of analysis.

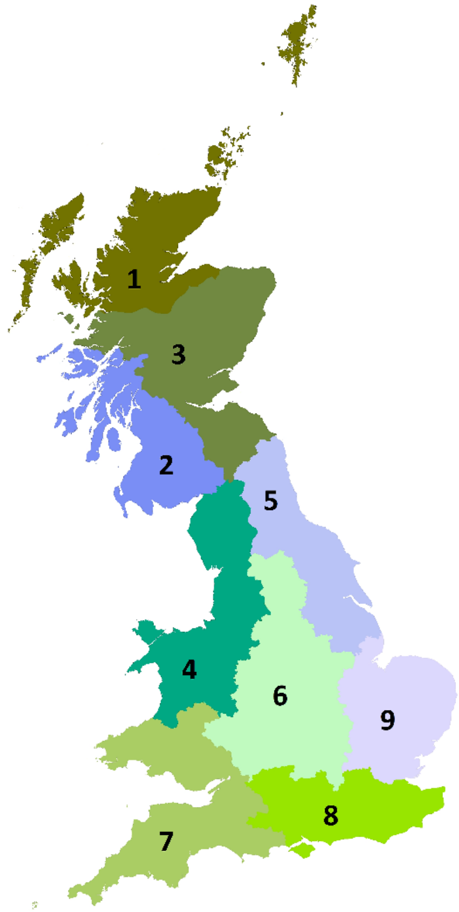

Figure 2.1: Climatic districts of Great Britain as defined by the UK Met Office. (1) Scotland north, (2) Scotland west, (3) Scotland east, (4) England northwest and northern wales, (5) northeast England, (6) Midlands, (7) southwest England and southern wales, (8) southeast England, (9) east Anglia

2.3.2.2 *Fight Against Blight Data*

Summary statistics of the FAB outbreak data were computed to evaluate variations in blight intensity across years and among climatic districts. Outbreaks were plotted on a postcode district polygon map of Great Britain in ArcGIS to visualise the distribution of disease.

2.3.2.3 *Mapping of Smith Period Frequency and Outbreaks*

Inverse distance weighted (IDW) interpolation was employed in ArcGIS to create heat maps of Smith Period occurrence and performance (i.e., outbreaks receiving/not receiving alerts). The heat maps apply values to the pixels in between the known data values using a nearest neighbour technique (Johnston, Hoef, Krivoruchko & Lucas, 2001, Childs, 2004, Blanco, de Serres, Cárcaba, Lara & Fernández-Bustillo, 2012). Heat maps for the total number of Smith Periods during the study period were generated using the UKMO grid of 652 weather data points, and thus produced smooth surface plots. The outbreak data had an irregular distribution, due to the background patterning of potato crop locations, therefore a series of smoothing steps were used to create heat maps. If there were only one or two reported outbreaks at a location over the twelve-year study period those points were removed as they had a disproportionate impact on the weighting of the IDW map, especially in cases where there were relatively few neighbouring points. Maps from each smoothing step are shown to allow inspection of the impact of this technique on results.

2.3.2.4 Smith Period Alerts Prior to Outbreaks

The occurrence of a Smith Period alert prior to an outbreak was calculated using a 28-day window preceding the date the outbreak was reported. A 28-day period prior to the date that each outbreak was reported was considered to be sufficient for relating weather conditions to infection, and to incorporate variation and uncertainty in the outbreak data regarding the lay between disease occurrence and disease reporting. Results were presented by binning Smith Period occurrence into 0–7, 0-14, 0-21 and 0-28 days prior to the reported outbreak. The number of outbreaks not receiving an alert in the entire 28-day window within each year and region were also calculated.

The analysis was also completed for one day of Smith criteria rather than the full two-day period. This is breaking down the Smith Period to smaller elements to allow for clearer understanding of the occurrence of these criteria on a single day prior to risk periods.

2.3.2.5 Receiver Operator Characteristic Curve Analysis

Receiver operator characteristic (ROC) analysis was applied to evaluate the performance of the Smith Period (Fawcett, 2006). ROC curves are a graphical method of evaluating diagnostic tools with a binary classification system. The binary classification system was defined as: 1 = risk alert and 0 = no risk alert prior to an outbreak. A ROC curve is created by plotting the true positive rate (TPR) against the false positive rate (FPR) as the threshold criterion used to define a positive classification (an alert) is varied. To create a series of threshold criteria, we investigated the effect of varying the time lag, *k* (days), between an alert and an outbreak on the predictive success of the model. We considered a 28-day window prior to each outbreak as sufficient for relating weather conditions for late blight development to the dates at which disease was first observed in the crop. Thus, the presence or absence, *F* (-), of an alert was determined as:

$$F(k) = \begin{cases} 1, & t \leq k \\ 0, & t > k \end{cases}$$

where k $\in$ {1, 2, 3... 28}, and t (days) is time.

Data were grouped by year and climatic district and the proportion of outbreaks that received an alert (1) on each of the days (1-28) prior to the date disease was reported, and the proportion that did not (0) was computed. These ‘empirical probabilities’ were used as a series of 56 threshold criteria (28 values labelled as 1, and 28 values labelled as 0), also known as ‘cut-off values,’ to generate a set of 56 TPR and FPR values that form the coordinates of the ROC curve. To obtain the TPR and FPR values, a confusion matrix was calculated for each cut-off value (Table 2.1).

Table 2.1: Receiver operator contingency table classifications of true positive, false positive, false negative and true negative.

TP = proportion (1) > threshold	FN = proportion (1) <= threshold
FP = proportion (0) > threshold	TN = proportion (0) <= threshold

where TP = number of true positives, FP = number of false positives, FN = number of false negatives, and TN = number of true negatives. The TPR is then calculated as TP / (TP+FN) and the FPR = FP / (FP+TN). The performance of the Smith Period was then evaluated using the area under the ROC curve (AUROC). The AUROC serves as a single measure that summarises the performance of the Smith Period (i.e. the presence of an alert prior to reported outbreaks) across the full range of cut-off probabilities and takes values between 0.5 and 1.0 (Hanley & McNeil, 1982, Pencina, D'Agostino & Vasan, 2008, Rosner, 2015). In general, an AUROC of 0.5 suggests a diagnostic tool with no discrimination, 0.7–0.8 a 'fair' system, 0.8 – 0.9 a 'good' system and >0.9 an 'excellent' system (Hosmer, Lemeshow & Strurdivant, 2013). ANOVA of the AUROC was used to compare results between different climatic districts and years.

2.3.2.6 *Smith Period Alert Count*

The previous analysis considered if there was an alert prior to each outbreak but did not quantify the number of those alerts. We counted the number of alerts occurring within 7 and 14 days prior to outbreaks for both the full two-day smith period and for a single day of criteria. Results were categorised according to GB climatic districts and stages of outbreak.

2.3.2.7 *Temperature and Relative Humidity*

The previous analyses considered only Smith Period (2 days of favourable conditions for late blight) and the Smith Criteria (1 day of favourable conditions), which are an integrated metric for temperature and relative humidity conditions. We compared for each region and year, the raw data for the average minimum temperature and average duration of high relative humidity for each region and year for the 14 days prior to outbreaks.

2.4 RESULTS

2.4.1 UKMO Climatic Districts

There was notable variation in temperature, rainfall, and frost among the nine climatic districts of the UK during the study period (Figures 2.2-2.5). These summaries show that Scotland and southwest England and southern wales received the highest levels of rainfall, southern districts of England and Wales received the highest levels of sunshine, and temperatures begin to increase in Scotland later than in England and Wales each year. There was also notable temporal variation; e.g., 2007 and 2012 had higher amount of rainfall across all districts, whereas 2012 and 2013 had more air frost days in spring in all districts.

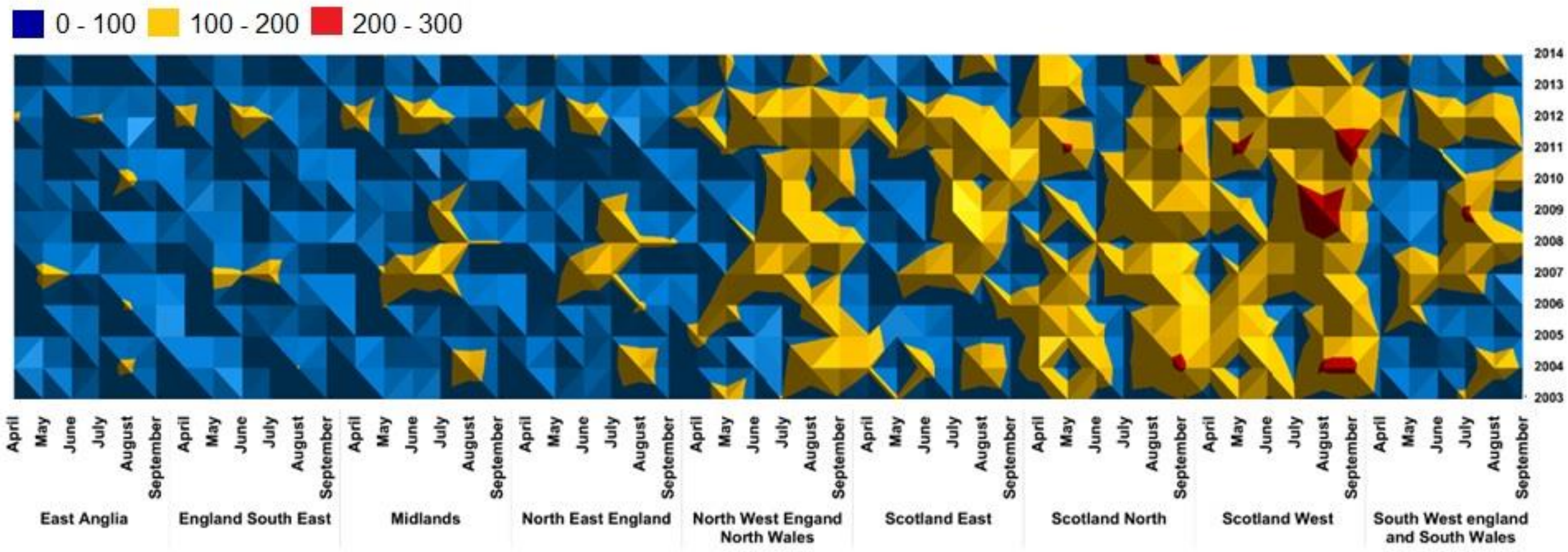

Figure 2.2: Summary of monthly rainfall (mm) for climatic districts of Great Britain from 2003 – 2014, sourced from United Kingdom Met Office

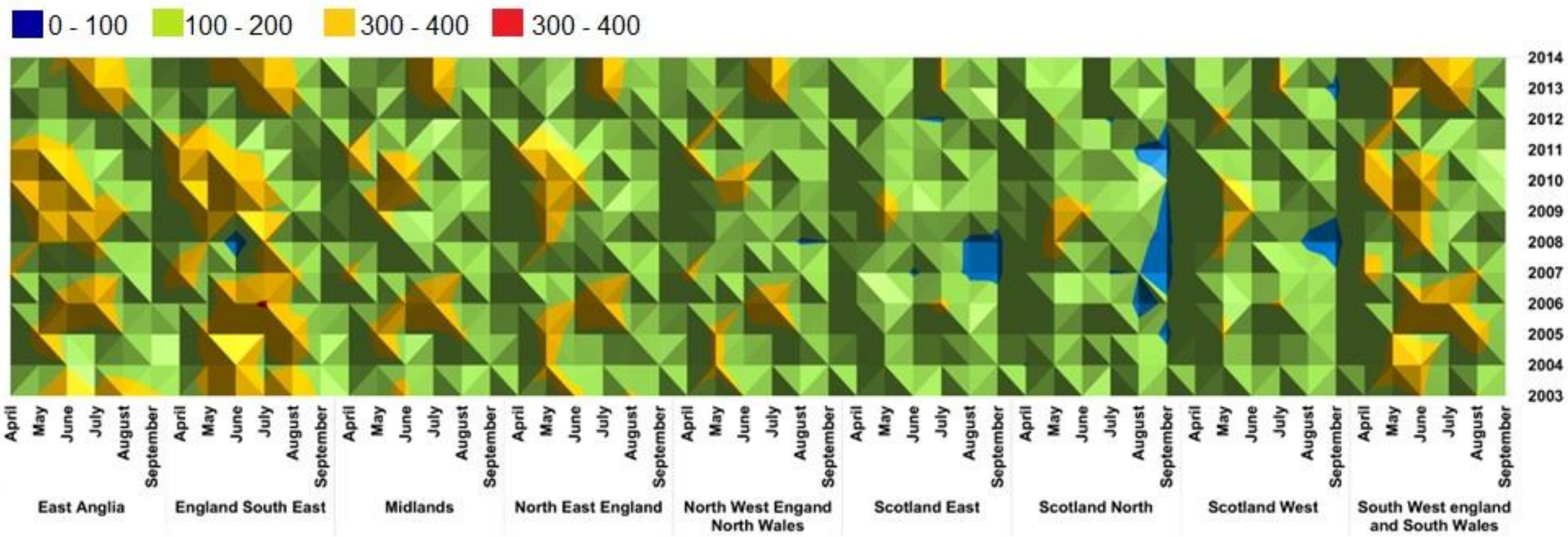

Figure 2.3: Summary of monthly sunshine hours for climatic districts of Great Britain from 2003 – 2014, sourced from United Kingdom Met Office

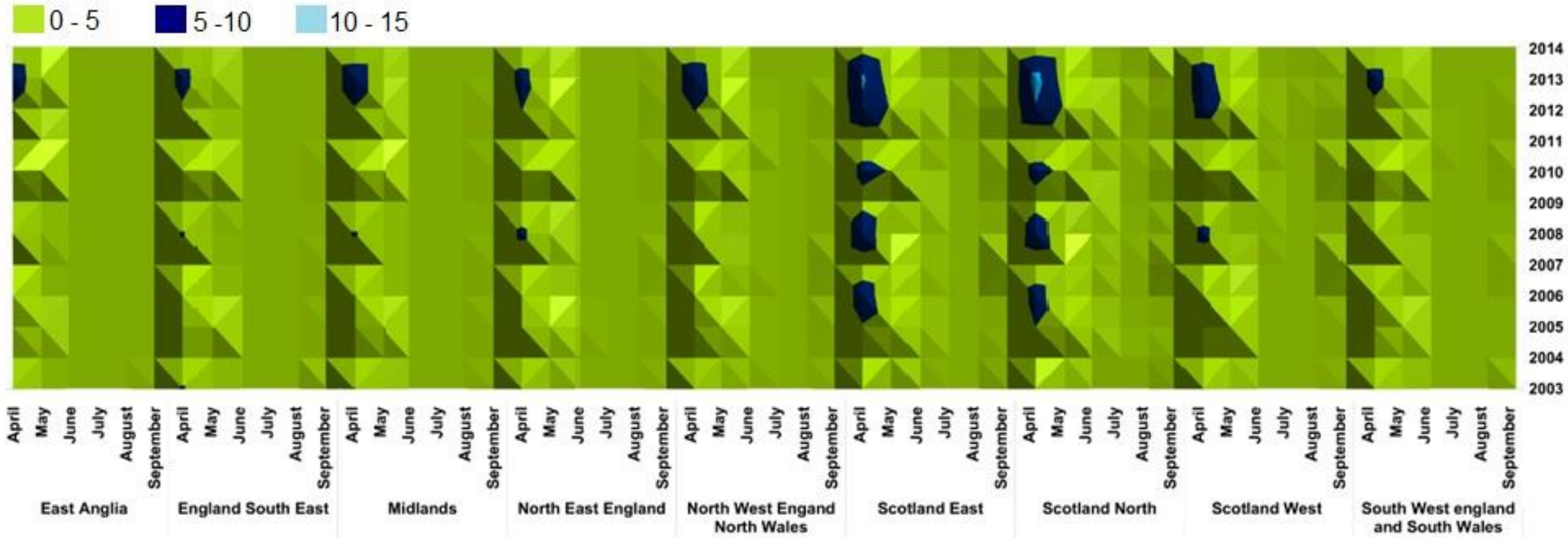

Figure 2.4: Summary of monthly number of air frost days for climatic districts of Great Britain from 2003 – 2014, sourced from United Kingdom Met Office.

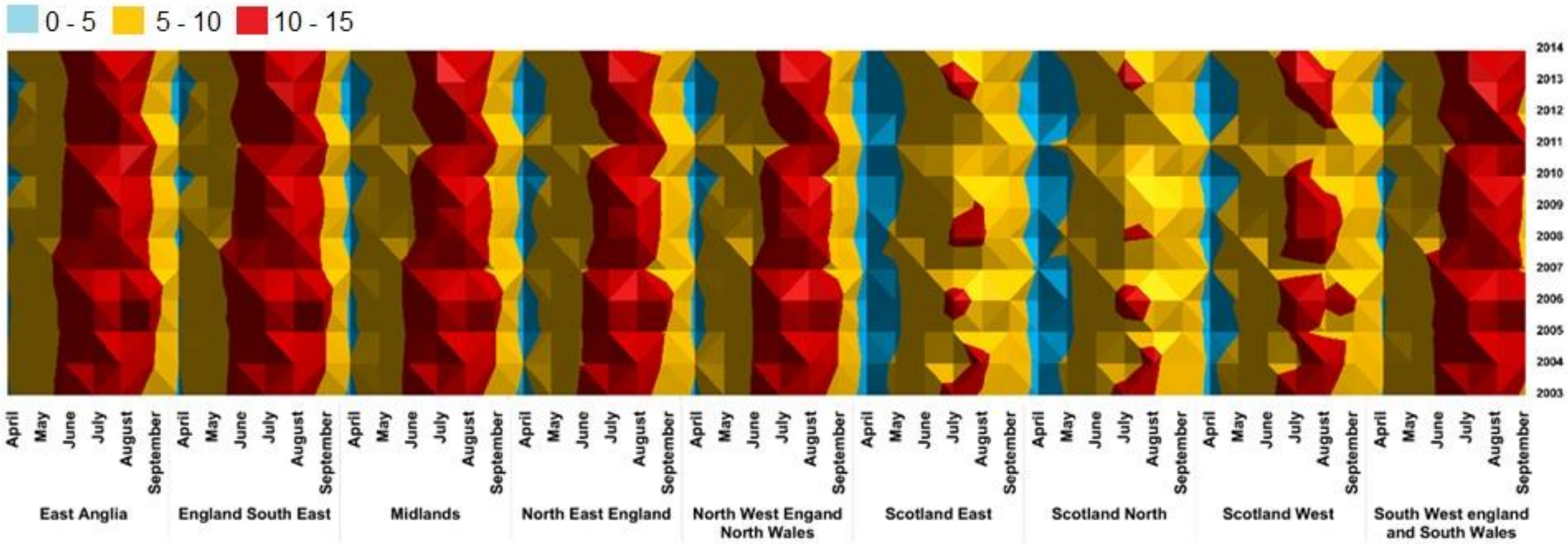

Figure 2.5: Summary of monthly minimum temperature data for climatic districts of Great Britain from 2003 – 2014, sourced from the United Kingdom Met Office

2.4.2 Fight Against Blight Data

There were >2000 potato late blight outbreaks recorded by FAB from 2003 – 2014 (Table 2.2). The highest levels of reported incidence occurred in 2007, 2012 and 2014 (>250 outbreaks), whereas the lowest levels of reported incidence occurred in 2005, 2010 and 2013 (< 100 outbreaks). These numbers corresponded with farmer and agronomist reports of 'bad years' due to above average rainfall that disrupted fungicide spray schedules and created conducive (humid) conditions for disease development. Mean reported incidence per year was 172 outbreaks.

Table 2.2: Fight Against Blight total recorded potato late blight outbreaks for 2003 - 2014

Year:	Outbreaks:
2003	104
2004	143
2005	99
2006	162
2007	281
2008	204
2009	143
2010	82
2011	179
2012	344
2013	66
2014	258

According to the FAB database there were outbreaks reported on over 50 different potato varieties during the study period. Maris Piper was the most common, reflecting its dominance in area planted in Great Britain, and accounted for 16% of all outbreaks reported. It has a low to moderate resistance rating to potato leaf blight of 4 according to the AHDB Potatoes varietal database.

There was notable variation in the spread of outbreaks across the nine different climatic districts: Scotland east (31%), East Anglia (19%), England northwest & Wales north (12%), England southwest & south Wales (11%), Midlands (11%), England northeast (7%), England southeast (6%), Scotland West (2%) and Scotland North (1%), (Figure 2.6). Scotland east had many reported outbreaks due to the density of potato production in that area. Stage of disease outbreak was most frequently recorded as ‘scattered’ (32%), with only 5% recorded as ‘severe’ or ‘very severe’ and 10% as single plant outbreaks. The majority (>50%) of outbreaks which recorded a source were from conventional/crops, with allotments, dumps, volunteers and organic farms making up 2, 2, 4 and 4% of recorded outbreaks, respectively.

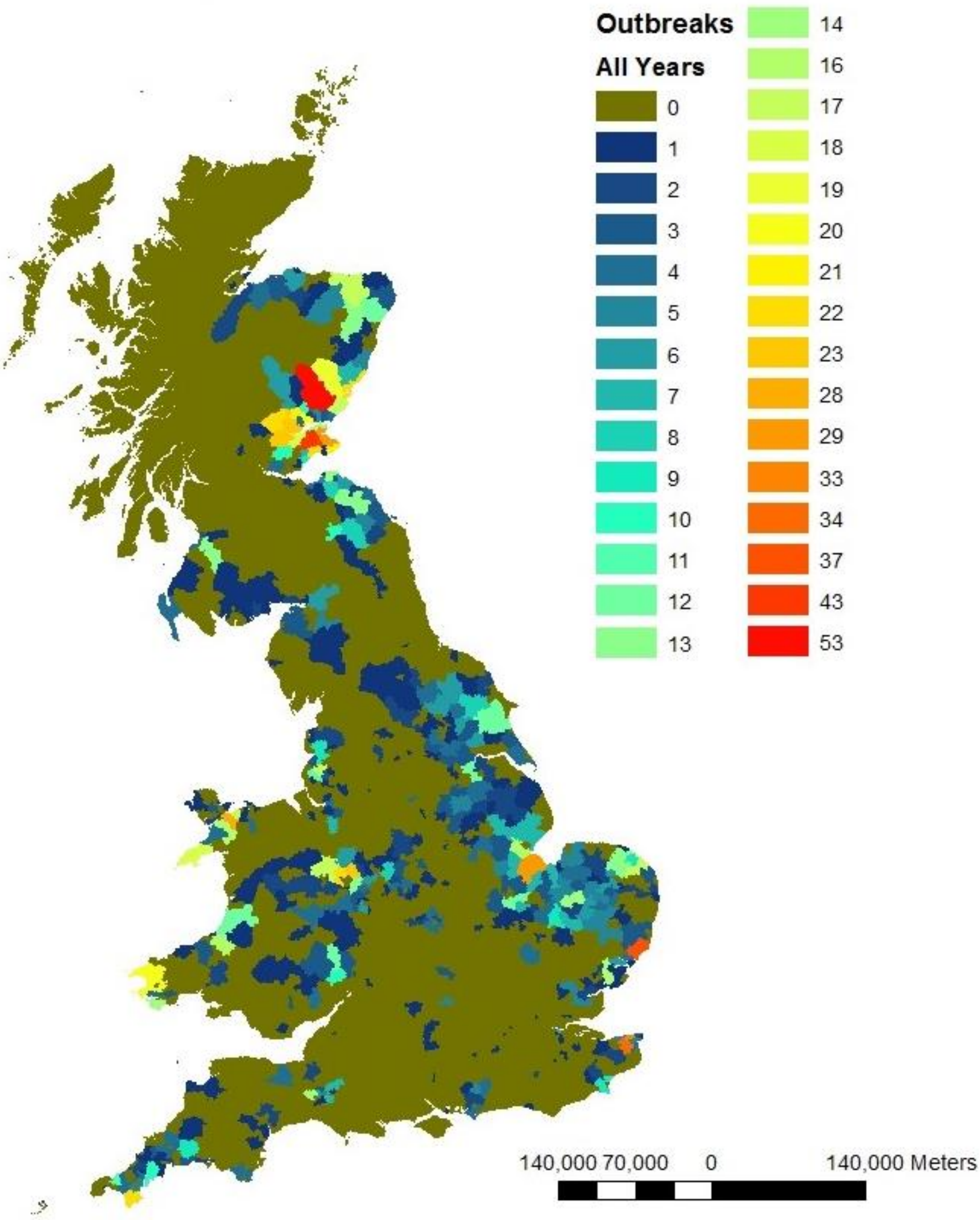

Figure 2.6: Potato late blight outbreaks from 2003 – 2014 mapped to their respective postcode districts with a count of outbreaks in each region indicated with a colour scale.

2.4.3 Smith Periods Alerts

IDW mapping of Smith Period occurrence revealed marked spatial variation in alert frequency; in particular coastal regions and southwest England & southern Wales received a large number of alerts (Figure 2.7). This acts as evidence to support use of a climatic regional analysis to understand the different climatological patterns across the country and their potential impact on decision support tools.

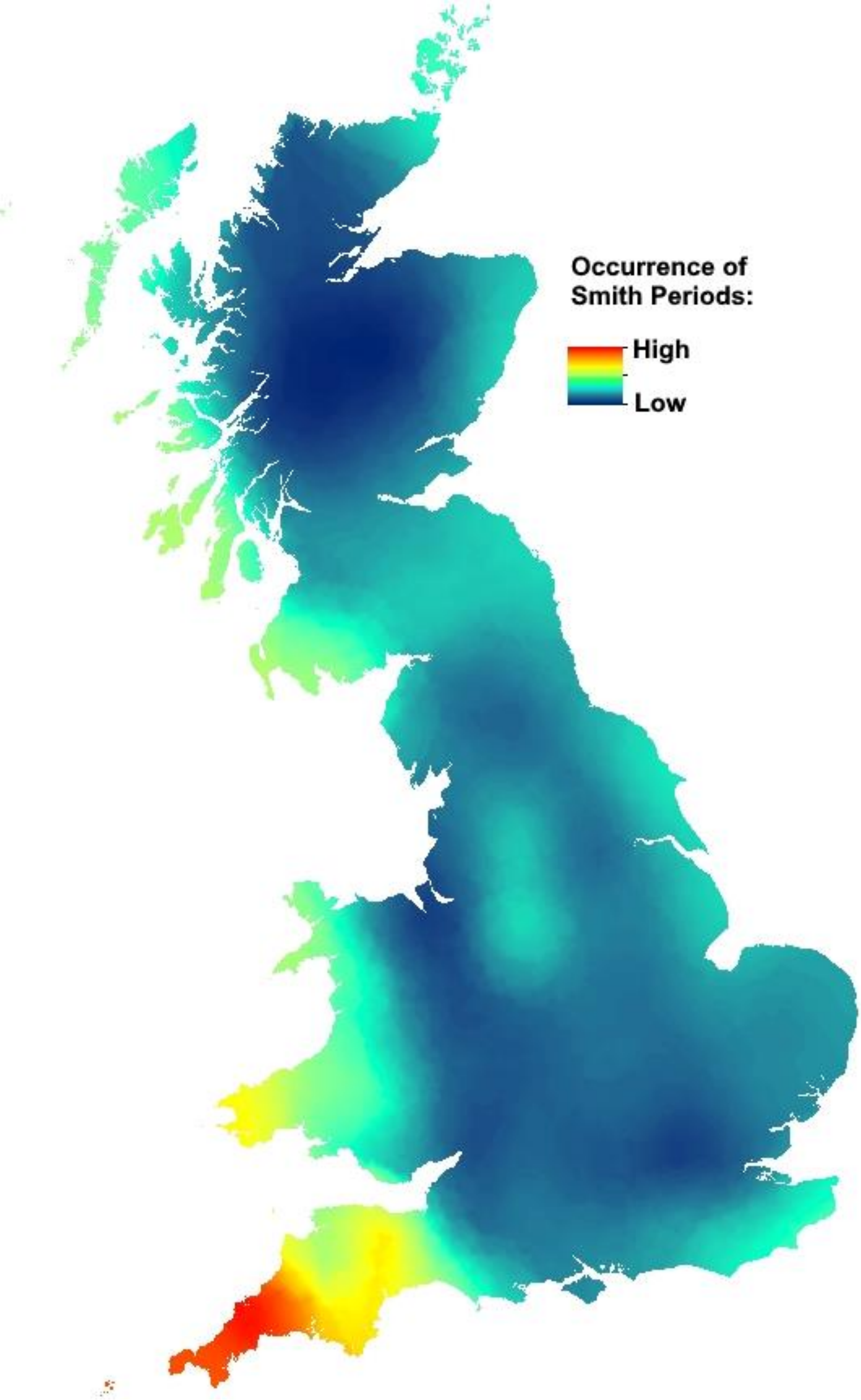

Figure 2.7: Inverse distance weighted map of Smith Period occurrences across Great Britain from April – September in 2003 – 2014. Surface was computed using data from 652 Met

Office location data points and shows the total number of Smith Periods during the study period.

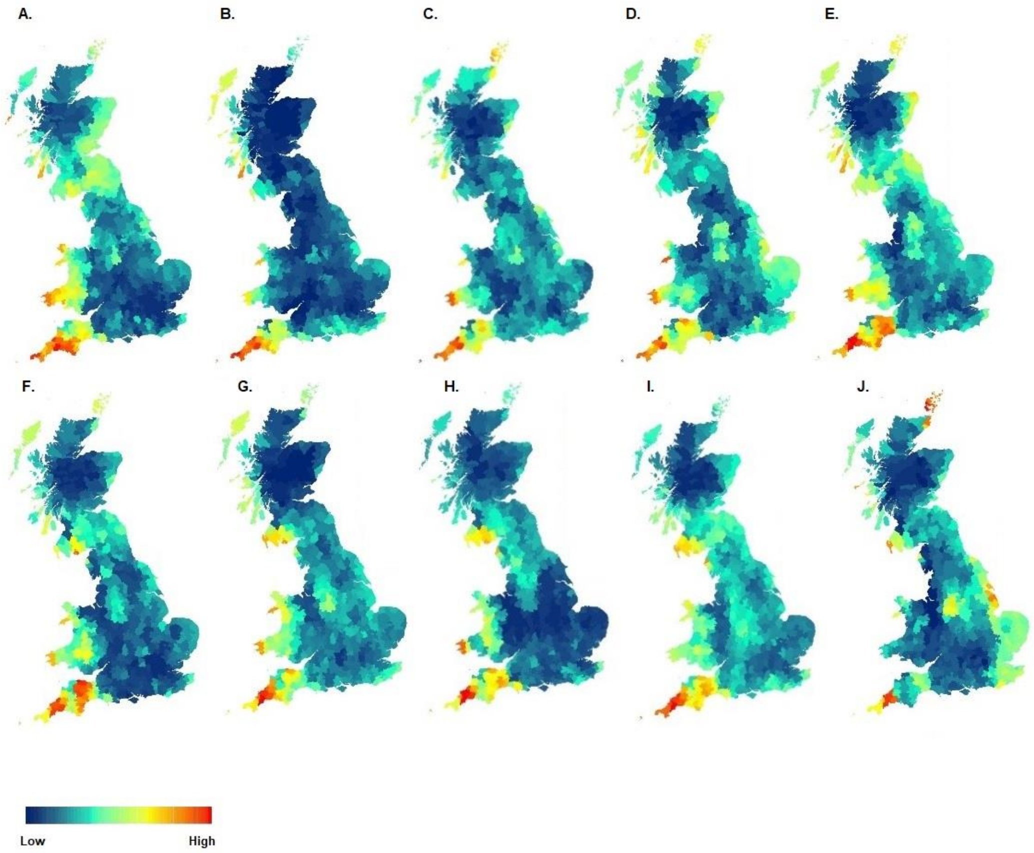

Figure 2.8: Inverse distance weighted maps of Smith Period occurrences across Great Britain for years (A) 2004, (B) 2005, (C) 2006, (D) 2007, (E) 2008, (F) 2009, (G) 2010, (H) 2011, (i) 2012, (J) 2014

Postcode district polygon maps of Smith Period occurrence (Figure 2.8) for specific years also showed regional variation in alert frequency, similar to the summary map for total alert frequency over the study period (Figure 2.7). The southwest still consistently received a higher number of Smith Period alerts each year in proportion with the rest of the country. The variation in frequency of alerts for districts between years, specifically more inland areas, confirms that risk varied between years.

Table 2.3 compares the total number of PLB outbreaks and Smith Periods in each region during the study period. Notably, the two adjoining districts England southwest & Wales south and England northwest & Wales north, had a similar number of outbreaks reported, but the more southerly district had more than double the number of Smith Period alerts. Also, of note, Scotland east and England northwest and Wales north received similar numbers of

Smith Period alerts, but Scotland east had more than double the number of outbreaks reported.

Table 2.3: Count of potato late blight outbreaks and Smith Periods for each climatic districts of Great Britain

Region:	Outbreaks:	Smith Periods:
Scot. N.	22	381
Scot. W.	41	1580
Scot. E,	678	4434
Eng. N. W. & W. N.	255	4282
Eng. N. E.	148	3788
Mid.	226	3668
Eng. S. W. & W. S.	243	10563
S. E. Eng.	113	2529
E. Anglia	392	3613
GB	2118	34838

2.4.4 Smith Period Alerts Prior to outbreaks

The relationship between recorded outbreaks and Smith Period occurrence at specific locations is summarised in Figure 2.9. The total number of potato late blight outbreaks for each year is shown along with the total number of Smith Period alerts and the percentage of outbreaks each year which specifically received a Smith Period alert 7, 14 and 21 days prior to the reported outbreak.

For 2007, 2008 and 2012 there were a large number of Smith Periods and also a large number of potato late blight outbreaks; these years were known to be very wet years (Figure 2.2), which explains the high number of Smith Periods called and may explain the high number of potato late blight outbreaks; in very wet years spray schedules for disease management may be disrupted and if the conditions are favourable for disease development then the risk of an outbreak may become high.

It is of interest to note the number of PLB outbreaks that did not receive an alert in the previous four weeks prior to disease detection (Figure 2.9). These data were further subdivided according to climatic district in Figure 2.10. Except for 2007 and 2012, described previously as being bad blight years but also high alert years due to heavy rainfall, the results show that approximately 20% of outbreaks in each year and district did not receive a risk alert in the previous 28 days. Southwest England south Wales is the region which consistently saw the fewest (<25%) of outbreaks which did not receive alerts. There was variation in East Anglia among years, but for 2003, 2006 and 2011 there were 58, 56 and 100% of outbreaks not receiving an alert in the previous 28 days, respectively. In eastern Scotland in 2004 over 52% of outbreaks did not receive an alert. In the Midlands in 2003, 2004, 2005, 2006 and 2014 approximately 50% of outbreaks did not receive an alert in the previous 28 days. In northeast England in 2005, 2008, 2011, 2013 and 2014 at least 40% of outbreaks did not receive an alert in the previous 28 days. In northwest England and north Wales in 2006, 2013 and 2014 more than 50% of outbreaks did not receive an alert in the 28 days prior to the outbreak being reported. Note that these analyses did not account for the intensity of potato production in each area, due to insufficient data.

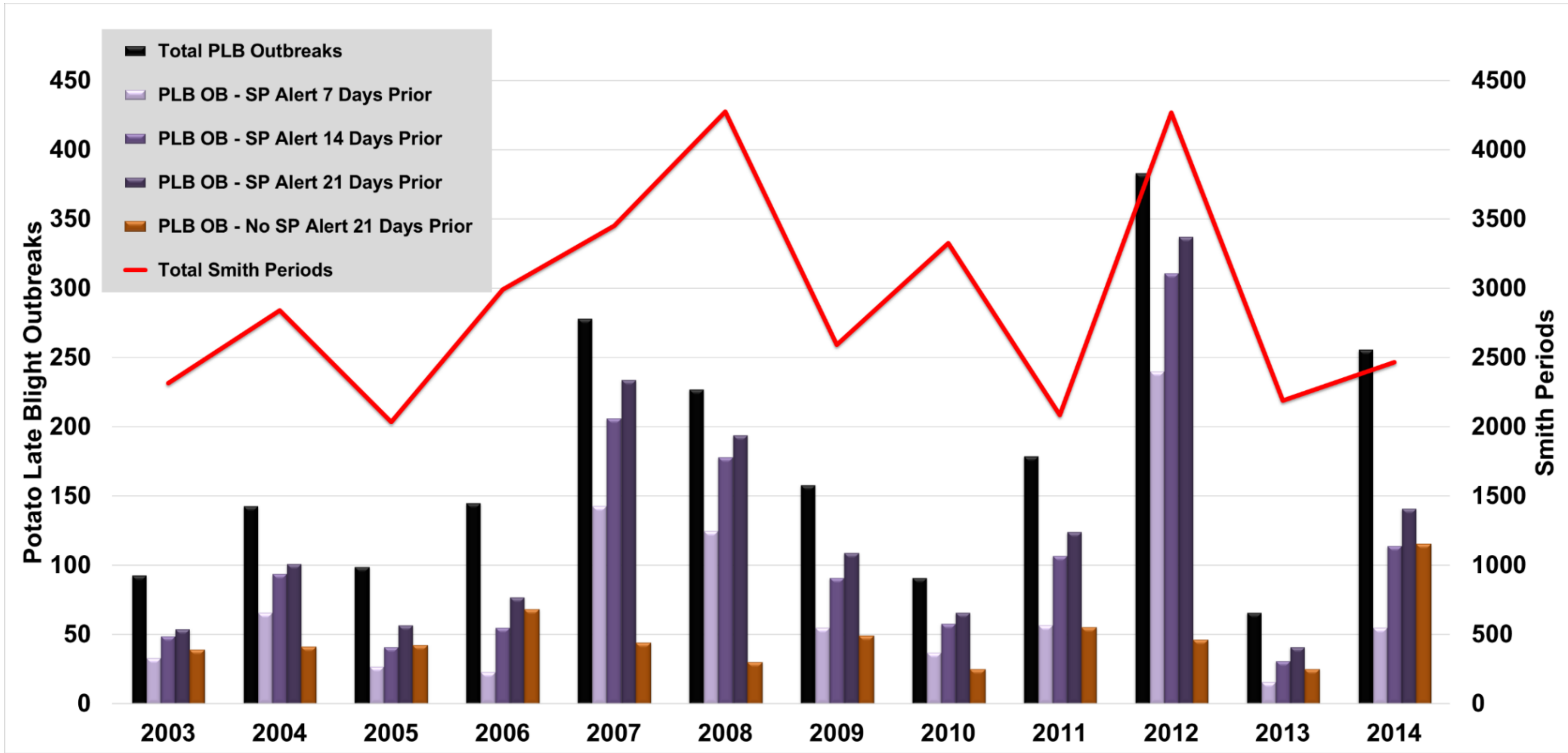

Figure 2.9: Total number of potato late blight outbreaks and the number receiving Smith Period alerts in the previous 7, 14 and 21 days or not at all. The secondary y-axis shows the total number of Smith Periods each year.

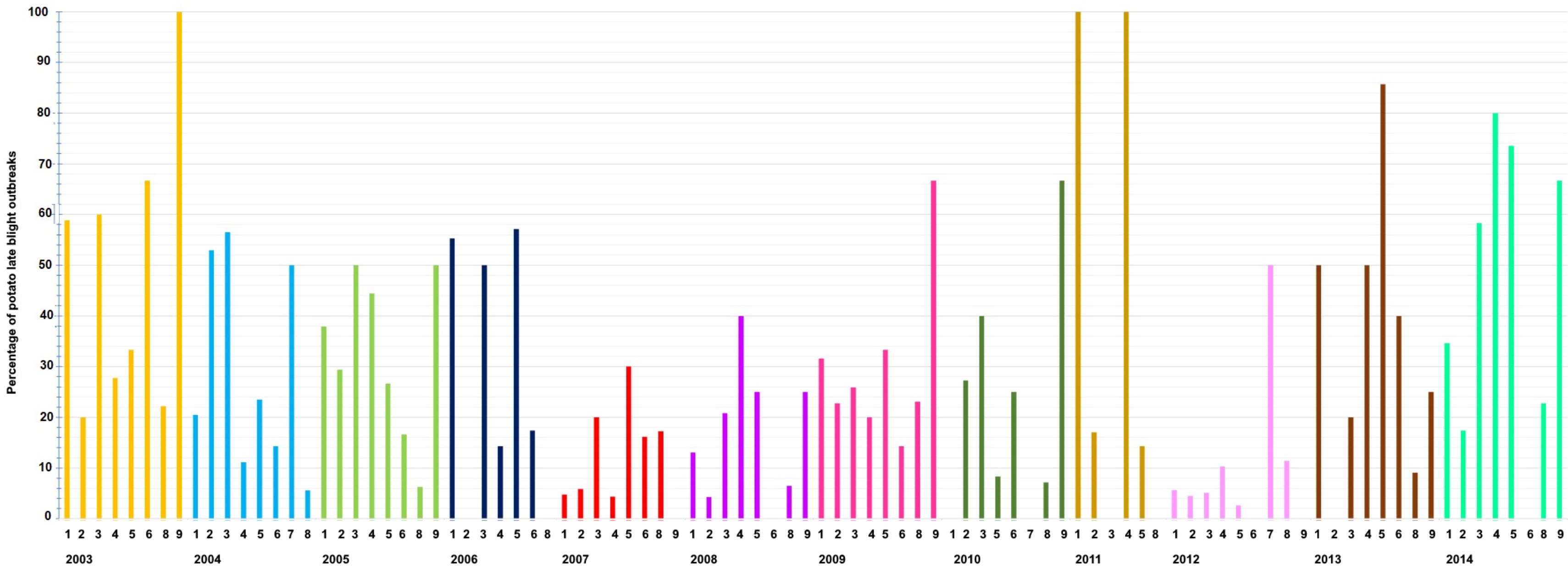

Figure 2.10: Proportion of outbreaks for each climatic district and year that did not receive a Smith Period alert in the 28 days prior to the date of observation. 1 = East Anglia, 2 = eastern Scotland, 3 = midlands, 4 = north east England, 5 = north west England and north Wales, 6 = south east England, 7 = Scotland north, 8 = south west England and southern Wales & 9 = western Scotland.

2.4.5 Mapping of PLB Outbreaks Receiving Smith Period Alerts

IDW interpolation maps were used to visualise Smith Period performance for 7, 14, 21, and 28 days prior to the date of disease observation (Figures 2.11 – 2.14 respectively. Seven days prior to alerts we see that the southwest of England and south Wales contain the highest number of outbreaks receiving alerts. This trend remains even with smoothing, removal of outbreak locations with only one alert (2.11.B) and removal of outbreak locations with two alerts (2.11.C) and poor performance is consistent across all three maps for northwest England and northern Wales and southeast England. Performance in the northeast of England reduces with the smoothing technique. We find these trends are consistent in Figure 2.12 and 2.13 for 14 and 21 days prior to the reported outbreaks. In Figure 2.14 we see that after 28 days there are established areas where there is a low frequency of alerts, around north west England and the western midlands of England.

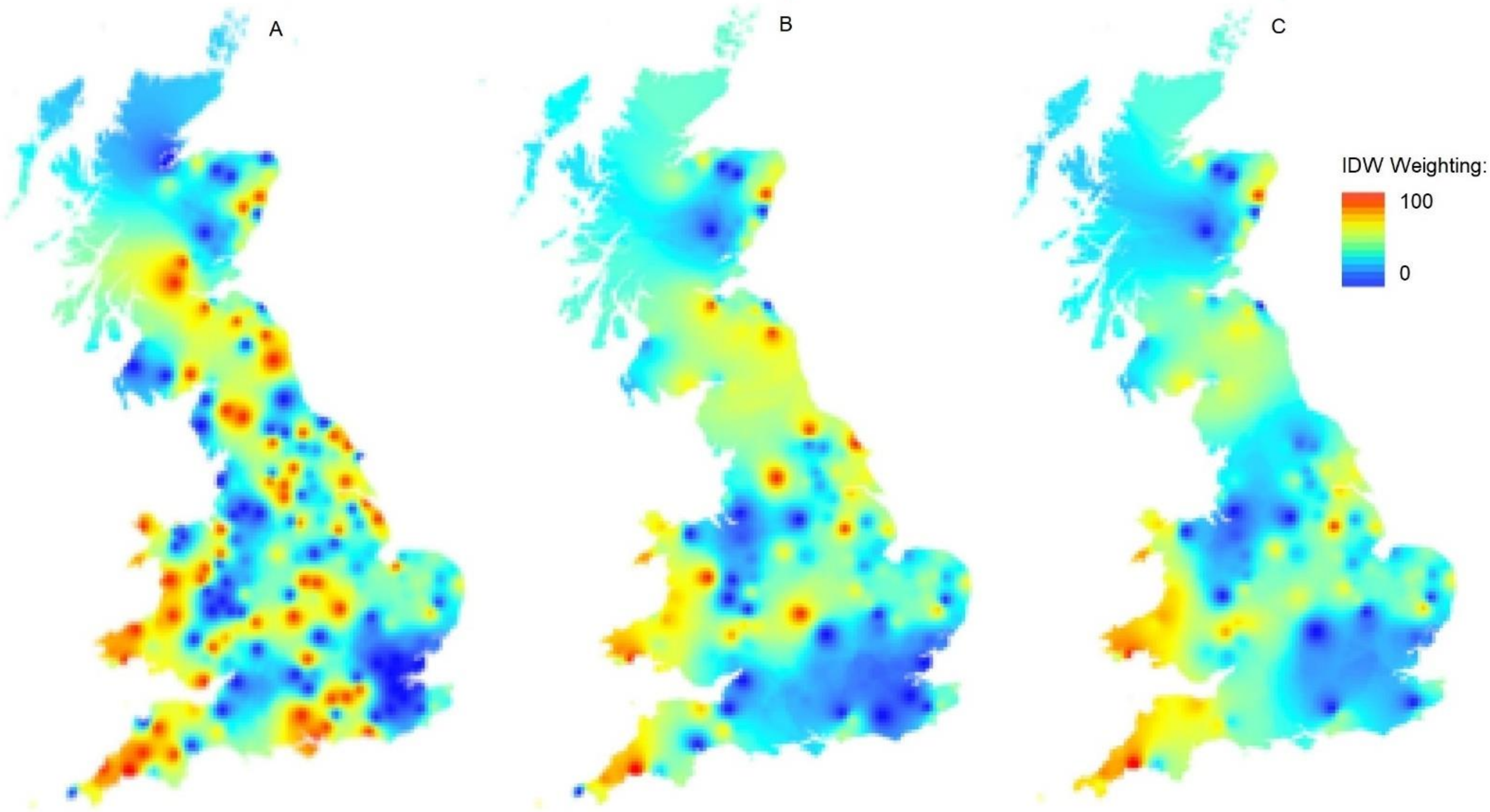

Figure 2.11: Inverse distance weighted maps showing total proportion of potato late blight outbreaks (2003 – 2014) that received a Smith Period alert in the 7 days prior to the outbreaks being reported, and those which did not. Red indicates a high number of outbreaks receiving an alert and blue indicates a low number of outbreaks receiving an alert. (A) All outbreak data, (B) locations with only one outbreak removed to smooth the data, (C) locations with only two outbreaks removed to further smooth the data.

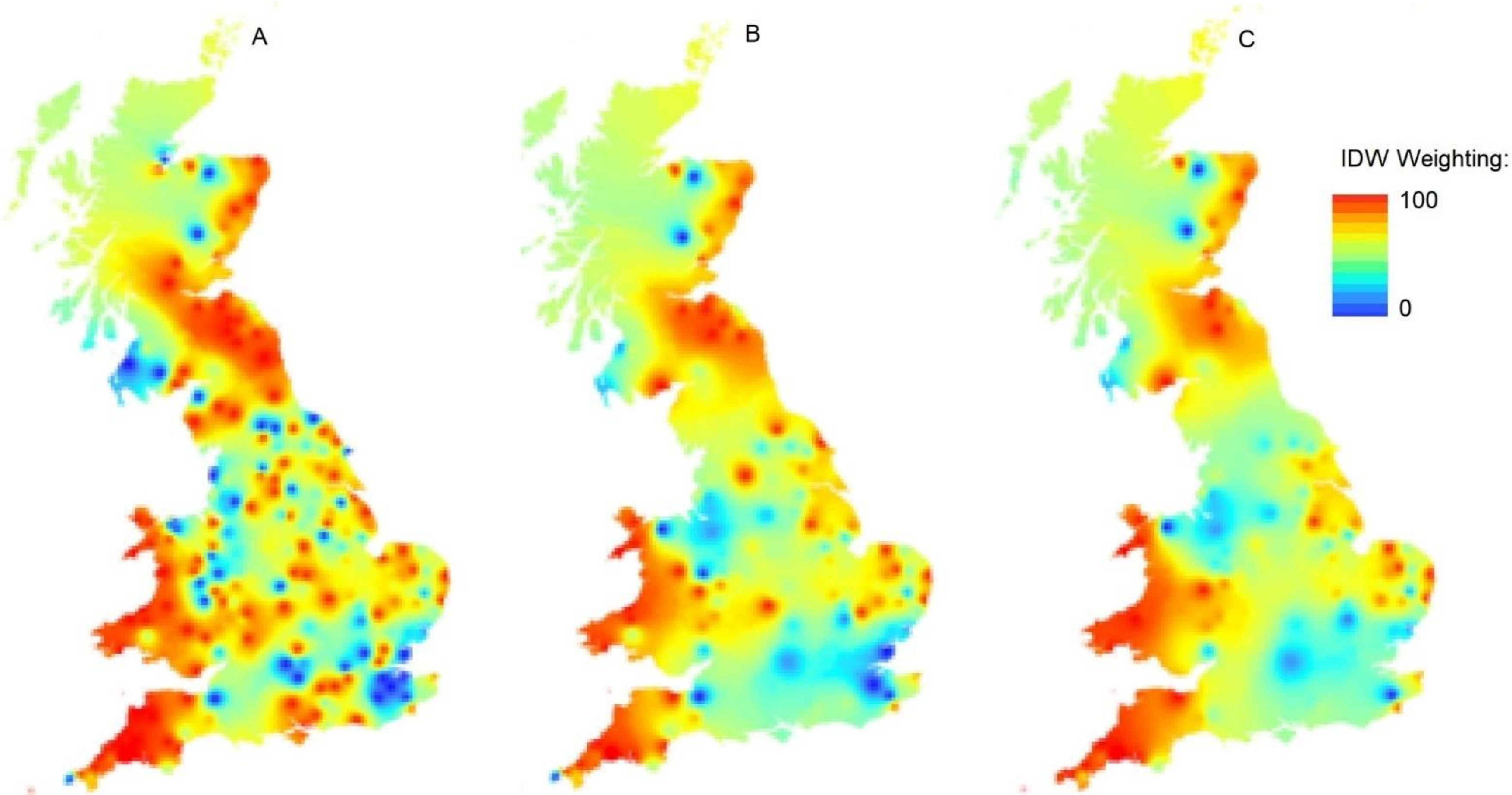

Figure 2.12: Inverse distance weighted maps showing total proportion of potato late blight outbreaks (2003 – 2014) that received a Smith Period alert in the 14 days prior to the outbreaks being reported, and those which did not. Red indicates a high number of outbreaks receiving an alert and blue indicates a low number of outbreaks receiving an alert. (A) All outbreak data, (B) locations with only one outbreak removed to smooth the data, (C) locations with only two outbreaks removed to further smooth the data.

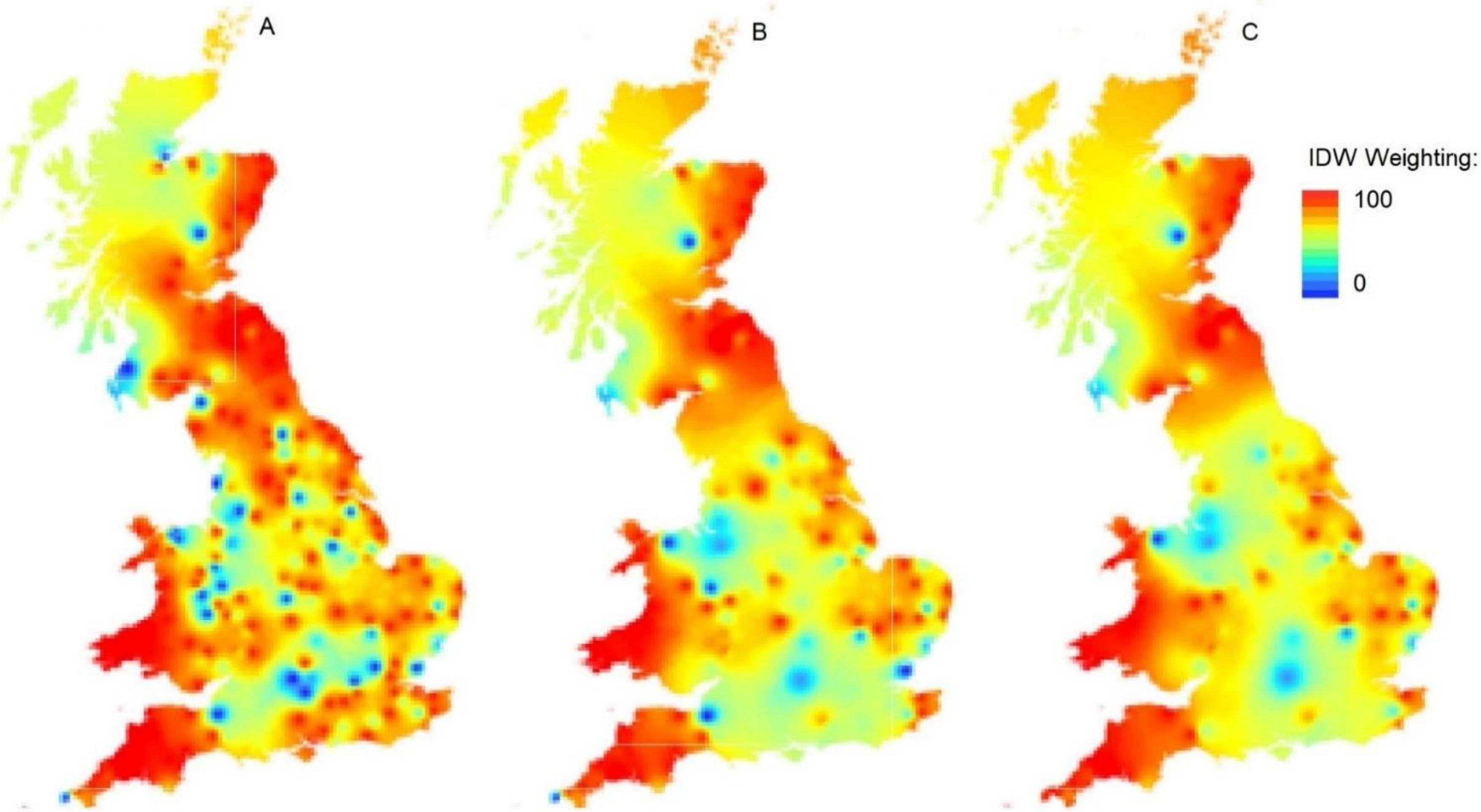

Figure 2.13: Inverse distance weighted maps showing total proportion of potato late blight outbreaks (2003 – 2014) that received a Smith Period alert in the 21 days prior to the outbreaks being reported, and those which did not. Red indicates a high number of outbreaks receiving an alert and blue indicates a low number of outbreaks receiving an alert. (A) All outbreak data, (B) locations with only one outbreak removed to smooth the data, (C) locations with only two outbreaks removed to further smooth the data.

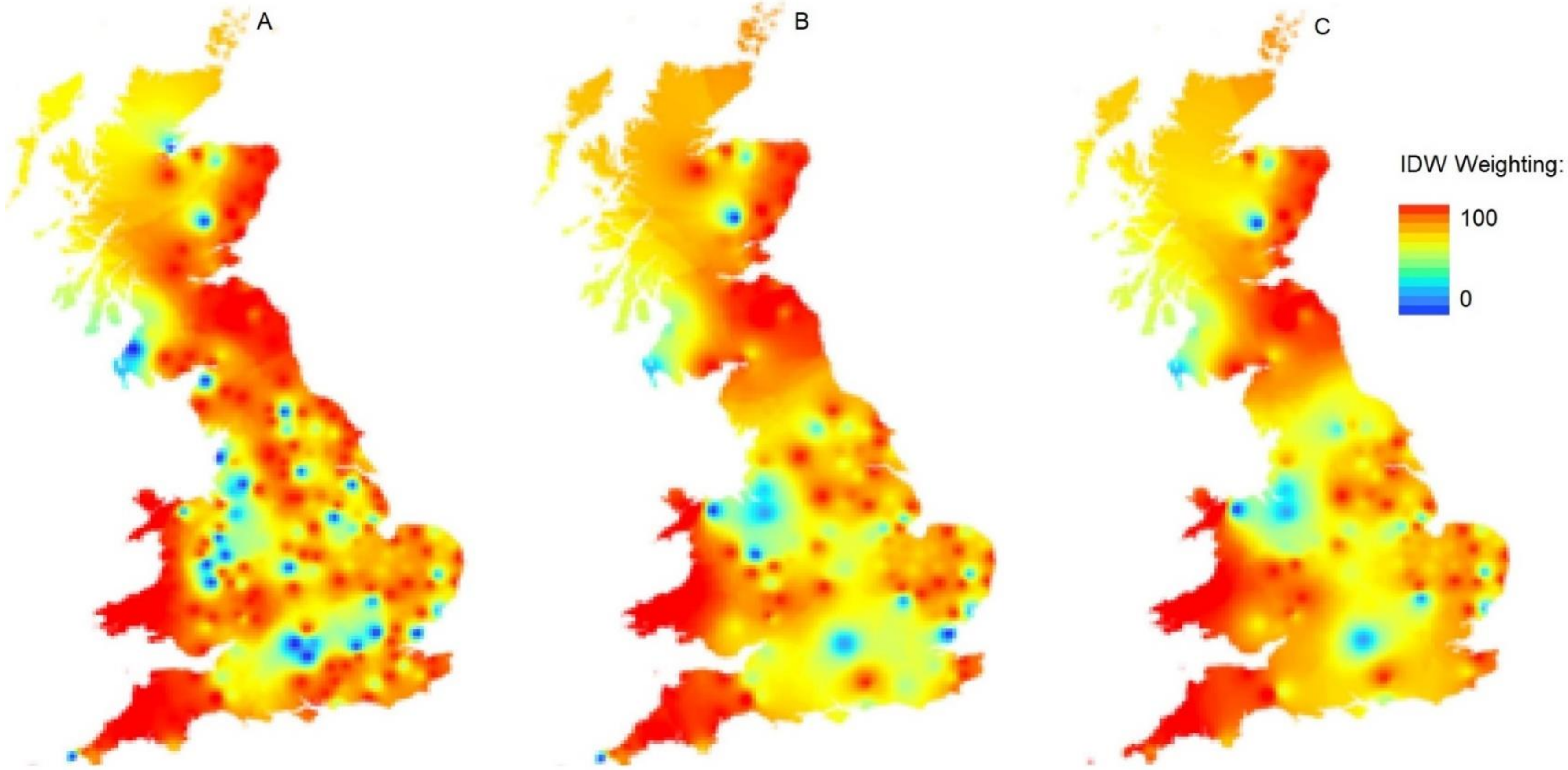

Figure 2.14: Inverse distance weighted maps showing total proportion of potato late blight outbreaks (2003 – 2014) that received a Smith Period alert in the 28 days prior to the outbreaks being reported, and those which did not. Red indicates a high number of outbreaks receiving an alert and blue indicates a low number of outbreaks receiving an alert. (A) All outbreak data, (B) locations with only one outbreak removed to smooth the data, (C) locations with only two outbreaks removed to further smooth the data.

2.4.6 Receiver Operator Characteristic Curve Analysis

The AUROC of the Smith Period for the entire dataset was 0.686 (95% CI = 0.540–0.832), indicating a ‘fair’ diagnostic tool for indicating high risk conditions for PLB development (Figure 2.15).

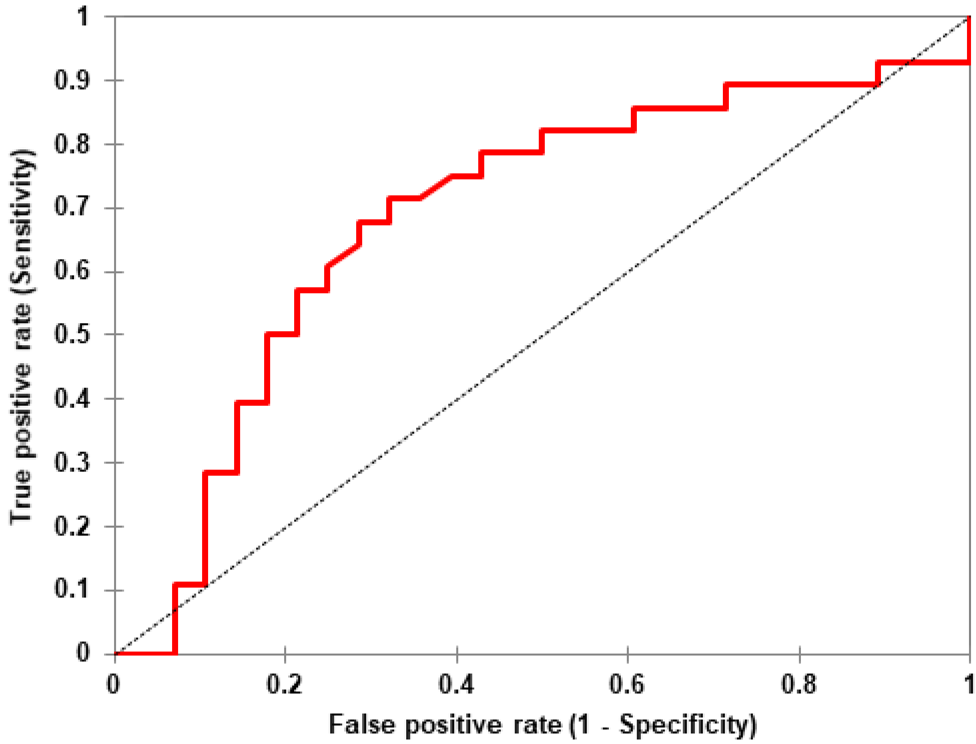

Figure 2.15: Receiver operator characteristic curve of the Smith Period for indicating high risk conditions for potato late blight, constructed using Fight Against Blight outbreak data from 2003 – 2014 for all Great Britain.

Large variation in Smith Period performance across GB was revealed when ROC curves were constructed for individual climatic districts (Figure 2.15). Scotland north was not included here due to the very small number of outbreaks that occurred between 2003 - 2014. AUROC was ranked from highest to lowest in the following order: (1) South West England and South Wales = 0.943 (95% CI = 0.892 – 0.995), (2) South East England = 0.766 (95% CI = 0.638 – 0.894), (3) Eastern Scotland = 0.740 (95% CI = 0.607 – 0.872), (4) North East England = 0.684 (95% CI = 0.539 – 0.828), (5) Midlands = 0.628 (95% CI = 0.467 – 0.790), (6) East Anglia = 0.520 (95% CI = 0.362 – 0.679), (7) North West England and North Wales = 0.443 (95% CI = 0.288 – 0.597), (8) Western Scotland = 0.225 (95% CI = 0.108 – 0.343).

ANOVA analysis comparing AUROC values showed that year and region were significant factors affecting performance of the Smith Period, Year: [F (11,75) = 3.26, p = 0.001], Region: [F (8,75) = 3.62, p = 0.001].

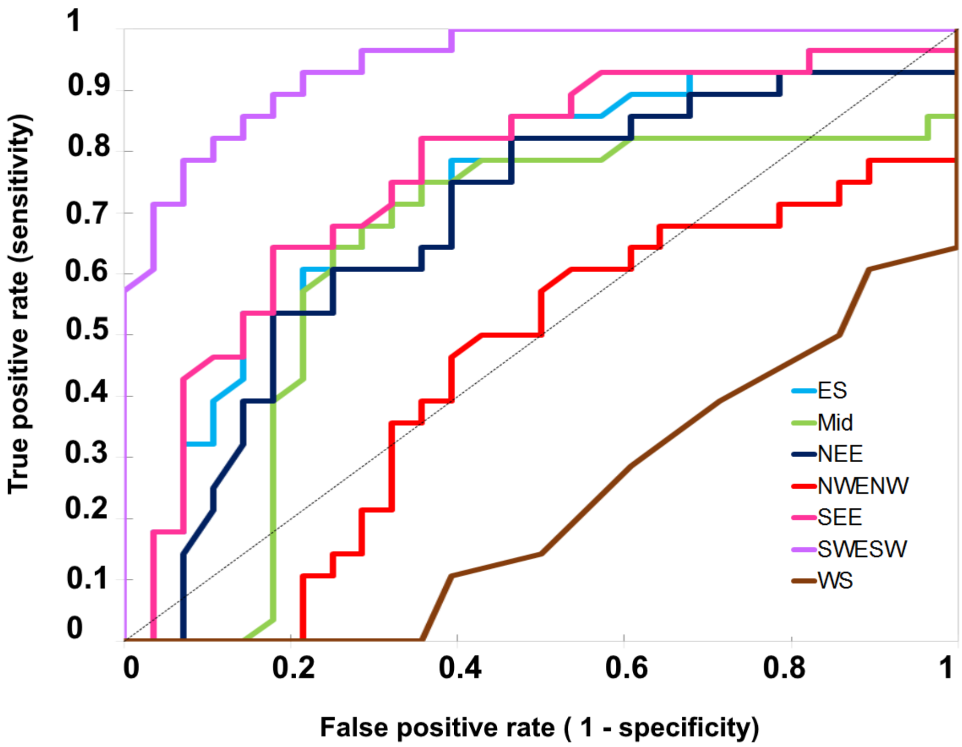

Figure 2.16: Receiver operator characteristic curves of the Smith Period for indicating high risk conditions for potato late blight, constructed using Fight Against Blight outbreak data from 2003 – 2014 grouped into climatic districts.

ROC curves for Smith Period performance within years and climatic districts revealed notable temporal and spatial variation (Figure 2.16). A summary of AUROC values from Figure 2.17 is given in Table 2.3. ANOVA analysis comparing AUROC values showed both year and region as highly significant factors affecting Smith Period performance, Year: [F (11,75) = 3.26, p = 0.001], Region: [F (8,75) = 3.62, p = 0.001]. Patterns in performance within region and year can be seen in the structure of the ROC curves and associated AUROC values. It can be seen that there are certain years where the Smith Period was an excellent alert system in each climatic district, e.g., 2012 (Figure 2.17(J)). There were, however, other years where there was notable variation in performance among districts, e.g., 2009 and 2013 (Figure 2.17 (G) & (K)). It is important to note that AUROC values were generally high for southwest England and southern wales, where previous analyses have revealed a high frequency of alerts occurring; however, 2006, 2013 and 2014 have AUROC values of 0.61, 0.68 and 0.64, respectively. While these values do not denote a poor diagnostic tool, they suggest that there is the possibility to improve the Smith Period.

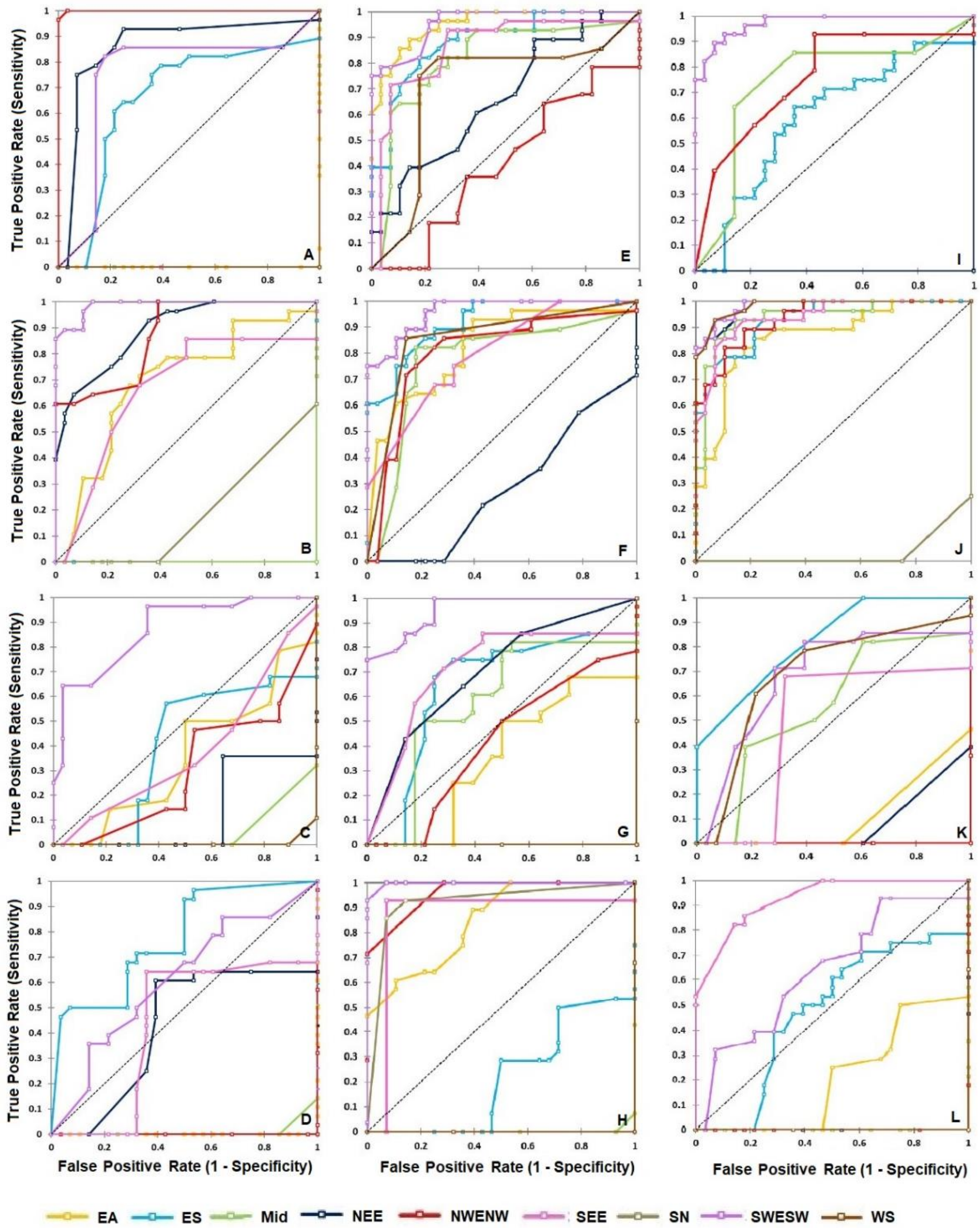

Figure 2.17: Receiver operator characteristic curves of the Smith Periods for indicating high risk conditions for potato late blight, constructed using Fight Against Blight outbreak data grouped by climatic district and year, (A) 2003, (B) 2004, (C) 2005, (D) 2006, (E) 2007, (F) 2008, (G) 2009, (H) 2010, (I) 2011, (J) 2012, (K) 2013 and (L) 2014.

Table 2.3: AUROC Values quantifying the Smith Periods performance as a diagnostic tool for indicating high risk conditions for potato late blight, calculated from Fight Against Blight outbreak data for each climatic region and year, * = no data.

YEAR/REGION:	SN	SW	SE	NEE	NWENW	Mid	SWESW	SEE	EA
2003	*	0	0.66	0.86	1	0	0.75	0	0
2004	0.18	*	0	0.98	0.87	0	0.99	0.67	0.69
2005	*	0.01	0.4	0.13	0.31	0.05	0.87	0.39	0.36
2006	*	*	0.77	0.43	0	0.01	0.61	0.43	0
2007	*	0.71	0.89	0.66	0.41	0.82	0.96	0.86	0.95
2008	*	0.86	0.92	0.28	0.81	0.77	0.96	0.8	0.82
2009	*	0	0.64	0.7	0.42	0.58	0.96	0.71	0.36
2010	0.92	0	0.22	*	0.96	0	1	0.86	0.85
2011	0.21	*	0.6	0	0.76	0.74	0.97	*	0
2012	0.03	*	0.93	0.98	0.94	0.94	0.98	0.94	0.86
2013	*	0.69	0.83	0.08	0	0.56	0.68	0.49	0.11
2014	*	0	0.48	0	0	0	0.64	0.93	0.21

The ROC analysis for each year and region was repeated looking at a single day of criteria rather than the full two-day Smith Period. Performance improved in many years and across many districts as one day of criteria will logically occur more frequently than two days; 2004, 2007, 2008, 2009, 2010, 2011 and 2012 all had AUC values > 0.9 (Table 2.4, Figure 2.18). Variation in performance among districts was still evident in 2003-2006, 2013 and 2014 with several AUROC values below 0.8. ANOVA analysis comparing the AUROC values showed both year and region as significant factors affecting

Smith period performance, Year: [F (11,74) = 3.54, p = <0.001], Region: [F (8,74) = 2.67, p = 0.013].

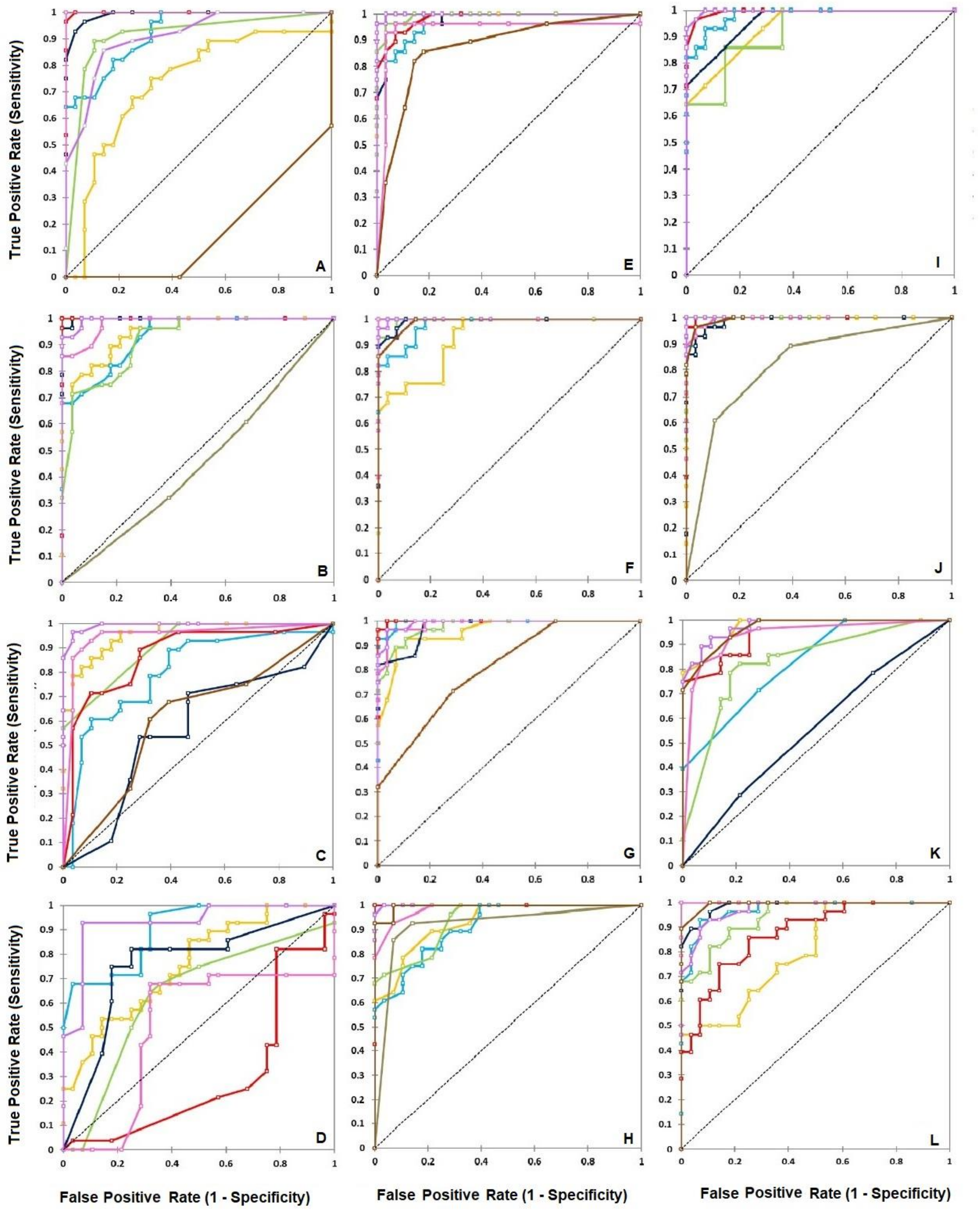

Figure 2.18: Receiver operator characteristic curves to assess a single day of Smith Period criteria as a diagnostic tool for indicating high risk conditions for potato late blight, constructed using Fight Against Blight outbreak data grouped by climatic district and year, (A) 2003, (B) 2004, (C) 2005, (D) 2006, (E) 2007, (F) 2008, (G) 2009, (H) 2010, (I) 2011, (J) 2012, (K) 2013 and (L) 2014.

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Table 2.4: AUROC Values assessing a single day of Smith Period criteria as a diagnostic tool for indicating high risk conditions for potato late blight, calculated from Fight Against Blight outbreak data for each climatic region and year, * = no data.

YEAR/REGION:	SN	SW	SE	NEE	NWENW	Mid	SWESW	SEE	EA
2003	*	0.16	0.92	0.99	1	0.91	0.91	1	0.73
2004	0.45	*	0.93	1	1	0.92	1	0.98	0.95
2005	*	0.61	0.8	0.56	0.87	0.91	0.99	0.95	0.96
2006	*	*	0.9	0.76	0.3	0.63	0.93	0.5	0.76
2007	*	0.87	0.98	0.98	0.98	0.99	1	0.94	1
2008	*	0.99	0.98	0.99	1	1	1	1	0.93
2009	*	0.81	1	0.97	1	0.98	0.99	0.99	0.96
2010	0.92	1	0.91	*	1	0.94	1	0.99	0.93
2011	0.86	*	0.98	0.96	0.99	0.92	1	*	0.94
2012	0.82	*	0.99	0.99	1	0.99	1	1	1
2013	*	0.97	0.83	0.55	0.95	0.83	0.97	0.94	0.97
2014	*	0.99	0.97	0.99	0.87	0.94	0.97	1	0.8

2.4.7 Frequency of Smith Periods

The previous analyses considered whether an alert occurred prior to an outbreak, but not the frequency of alerts prior to an outbreak. Examination of the frequency analysis results show a greater number of alerts in southwest England and south Wales than the other districts, and at 14 days prior to an outbreak both Scotland North and Scotland West had the lowest number of alerts (Figure 2.19). The same trends were apparent when the district data were further subdivided by year (data not shown). Interestingly, the mean for all districts except South West England and South Wales were below one at the seven-day time point. At the 14-day time point east Anglia, Midlands, northeast England, Scotland west and Scotland north all showed means of

Smith Period occurrence below 1.

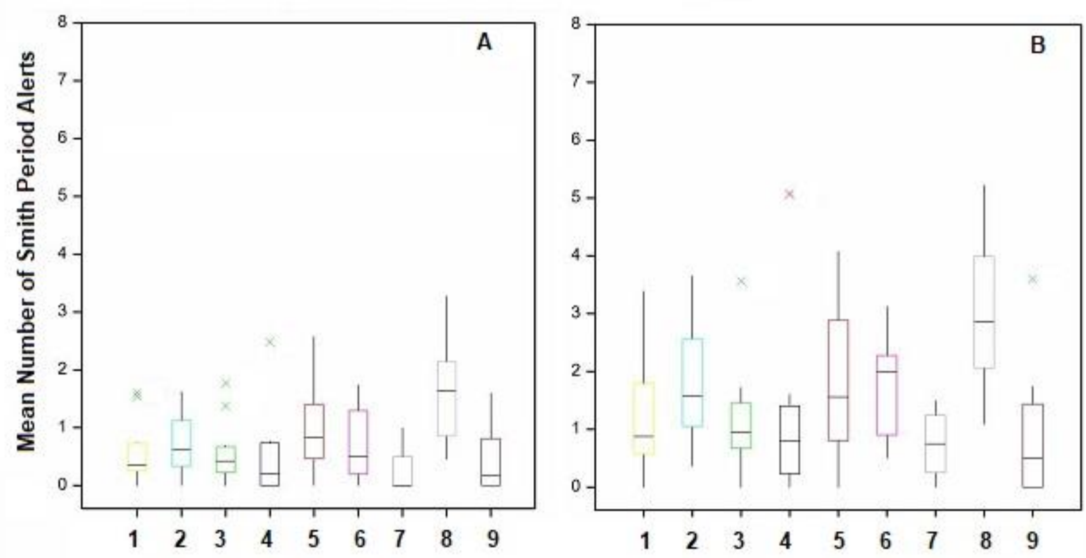


Figure 2.19: Mean number of Smith Periods (A) 7 days and (B) 14 days prior to date of observation of potato late blight outbreaks, grouped according to climatic region; (1) east Anglia, (2) eastern Scotland, (3) Midlands, (4) northeast England, (5) northwest England and north Wales, (6) southeast England, (7) Scotland North, (8) southwest England and south Wales and (9) Scotland north.

When examining the frequency of a single day of criteria, the results show that Scotland North was the only region to have a mean below one at 7 days prior to the outbreak; all other districts except for England southwest and Wales south had a mean frequency of between 1 and 2 alerts (Figure 2.20A). There was greater variation in the frequency of single days of criteria 14 days prior to an outbreak as this time window encompasses more data (Figure 2.20B). Notably, in northwest England and north Wales, area district where Smith Period performance was poor in the ROC analysis, the mean frequency of single days of criteria was relatively high at approximately 5 days receiving Smith Period alerts in the 14 days prior to outbreak.

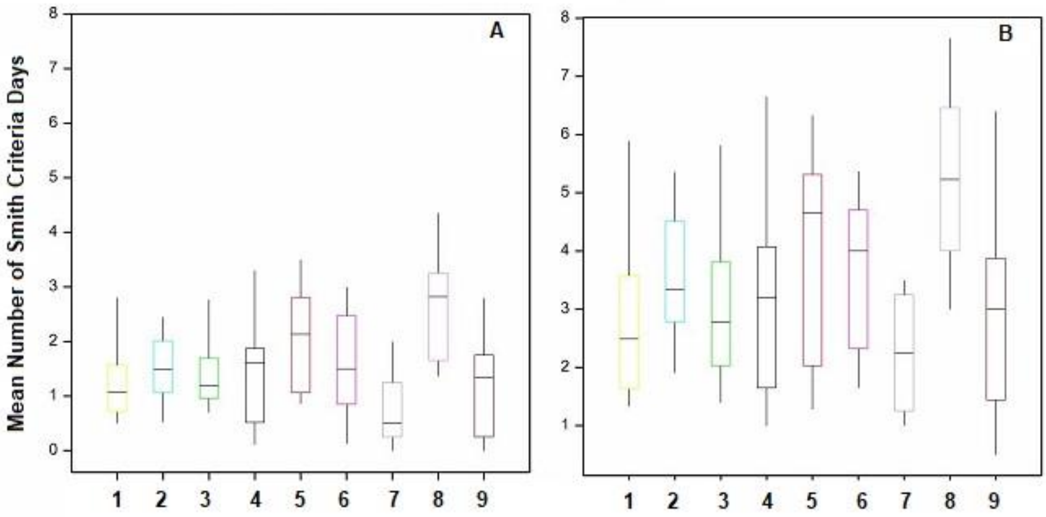


Figure 2.20: Mean number of days with one day of Smith Criteria (A) 7 days and (B) 14 days prior to prior to date of observation of potato late blight outbreaks from 2003 – 2014, grouped according to climatic district; (1) east Anglia, (2) eastern Scotland, (3) Midlands, (4) northeast England, (5) northwest England and north Wales, (6) southeast England, (7) Scotland North, (8) southwest England and south Wales and (9) Scotland north.

Frequency of alerts at 7 and 14 days prior to an outbreak for all disease stages was also computed: all (A), patch (P), scattered (SC), several patches (SP), severe (SV) and single plant (S) for 2004, 2006, 2008, 2012 and 2014, as these years had many outbreaks classified for disease stage. For both 7 and 14-days prior to outbreak detection in 2004, 2006 (14 day only), 2008 and 2014 the mean number of alerts for outbreaks classified as severe was greater than that for other stages of disease (Figure 2.21). Interestingly, for 2012, a year of heavy blight pressure, outbreaks classified as severe had a mean number of alerts prior to an outbreak below all other disease stage classifications. This indicates that for outbreaks classified as severe in years of normal blight pressure there is generally a higher frequency of risk periods prior to disease development. The difference seen in 2012 may be related to the high pressure felt that year and the resultant increase in inoculum load across the country.

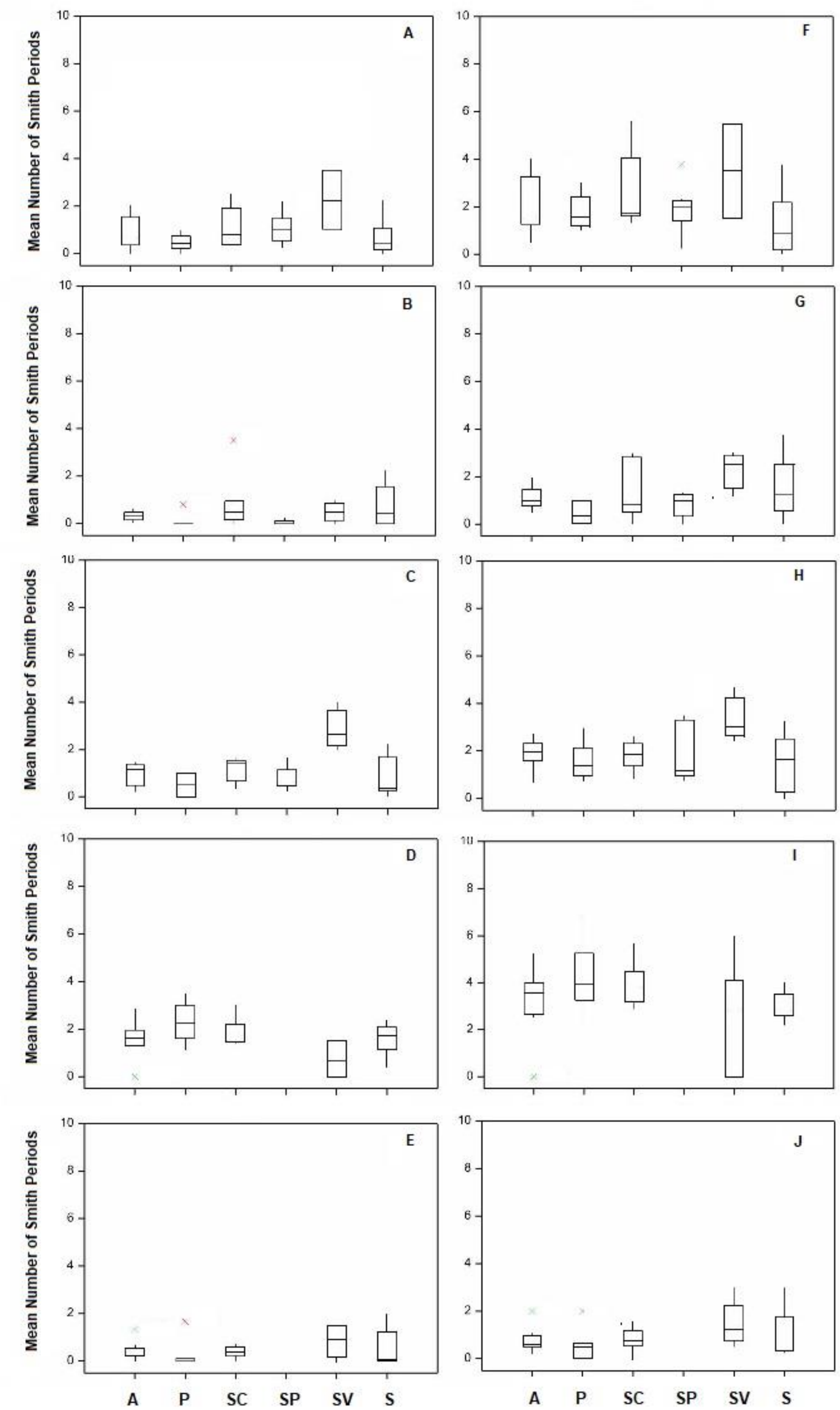


Figure 2.21: Mean number of Smith Period alerts that occurred prior to the date of observation of potato late blight outbreaks: (A) 7 days prior in 2004, (B) 7 days prior in 2006, (C) 7 days prior in 2008, (D) 7 days prior in 2012, (E) 7 days priors in 2014, (F) 14 days prior in 2004, (G) 14 days prior in 2006, (H) 14 days prior in 2008, (I) 14 days prior in 2012, (J)14 days prior in 2014. Each plot was subdivided to show outbreaks by reported stage of outbreak, A = all, P = patch, SC = scattered, SP = several patches, SV = severe and S = single plant. For each climatic region the mean of all climatic districts is shown.

Results for a single day of criteria 7 and 14 days prior to an outbreak, grouped according to disease stage, show the same trends as for the full

Smith Period (Figure 2.22). Except for 2012, there was a higher frequency of alerts for severe outbreaks, which is to be expected.

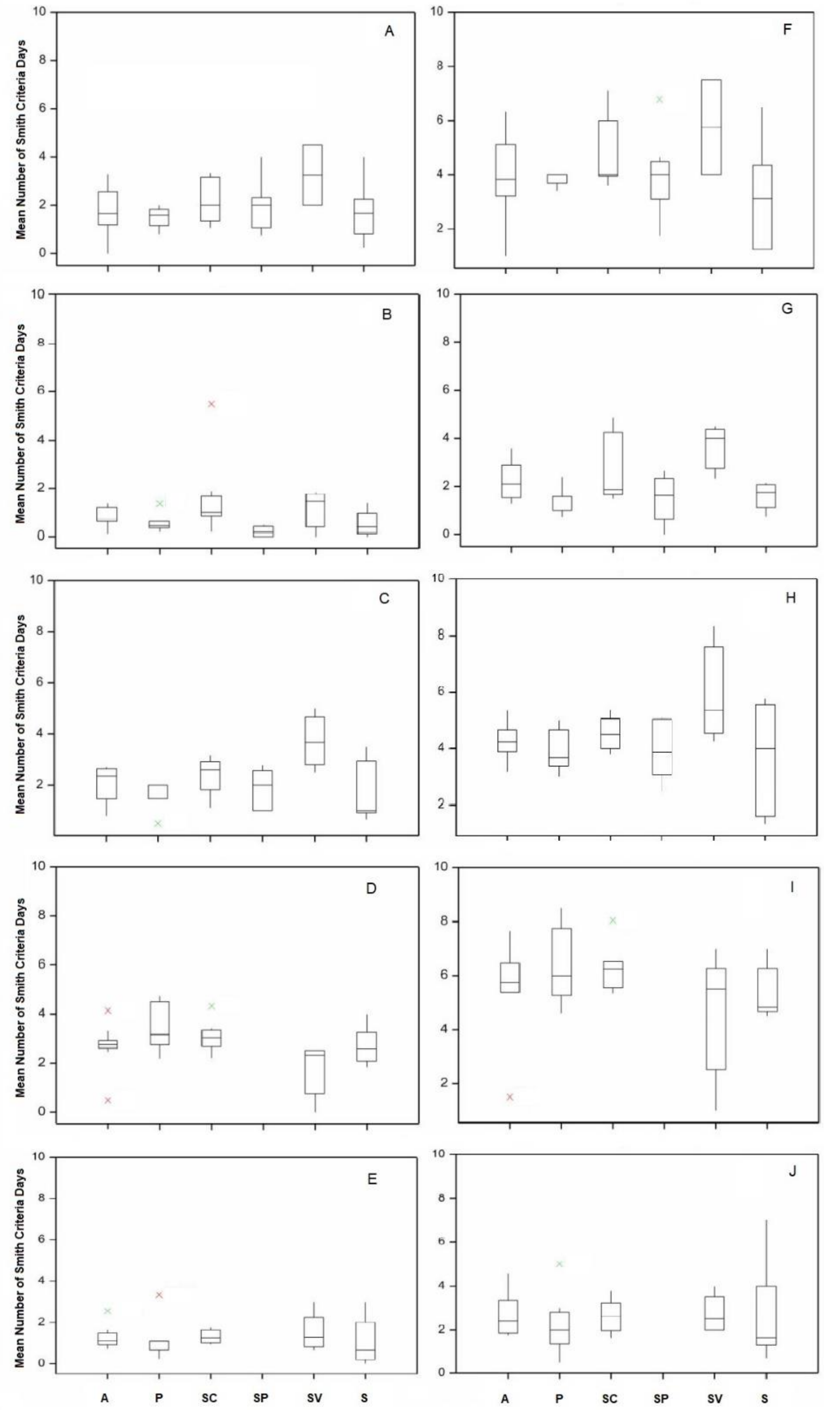


Figure 2.22: Mean number of days with one day of Smith Criteria which occurred prior to Fight Against Blight potato late blight outbreaks for (A) 7 days prior in 2004, (B) 7 days prior in 2006, (C) 7 days prior in 2008, (D) 7 days prior in 2012, (E) 7 days priors in 2014, (F) 14 days prior in 2004, (G) 14 days prior in 2006, (H) 14 days prior in 2008, (I) 14 days prior in 2012, (J)14 days prior in 2014. Each plot was subdivided to show outbreaks by reported stage of outbreak, A = all, P = patch, SC = scattered, SP = several patches, SV = severe and S = single plant. For each climatic region the mean of all climatic districts is shown.

2.4.8 Temperature and Relative Humidity

Thus far we have been evaluating the Smith Period and Smith Criteria as identifiers of risk for the development of potato late blight across all climatic districts of Great Britain for the years 2003 – 2014. This means looking at a set of temperature and relative humidity criteria combined for either a single or two-day period. It is of interest to separate out the temperature and relative humidity criteria to investigate if either individual criterion is being met predominately over another, or if there is no relationship. The individual criteria of the Smith Period are (1) a minimum temperature threshold of 10°C and (2) a duration of 11 hours of relative humidity ≥90%. We examined the proportion of outbreaks meeting each criterion (data not shown) for each year and climatic district with the most recent year 2014 as an example, (Figure 2.23) and the distribution of values in the Midlands as an example climatic district (Figure 2.24). Similar trends were seen across all years and in all districts, the mean daily minimum temperature within a 14-day window prior to reported potato late blight outbreaks for all districts was consistently above the 10°C temperature threshold and average number of hours of relative humidity ≥90% in the days prior to the reported outbreaks was consistently well below the 11-hour threshold. The temperature threshold means were only below the 10°C consistently in 2003 for south east England and 2004 and 2012 for Scotland north. The distribution of relative humidity duration in the days prior to reported outbreaks was skewed for all districts, except for North East England, towards the lower duration. The 11-hour threshold we have is often seen to be outside of the mean (Figure 2.24).

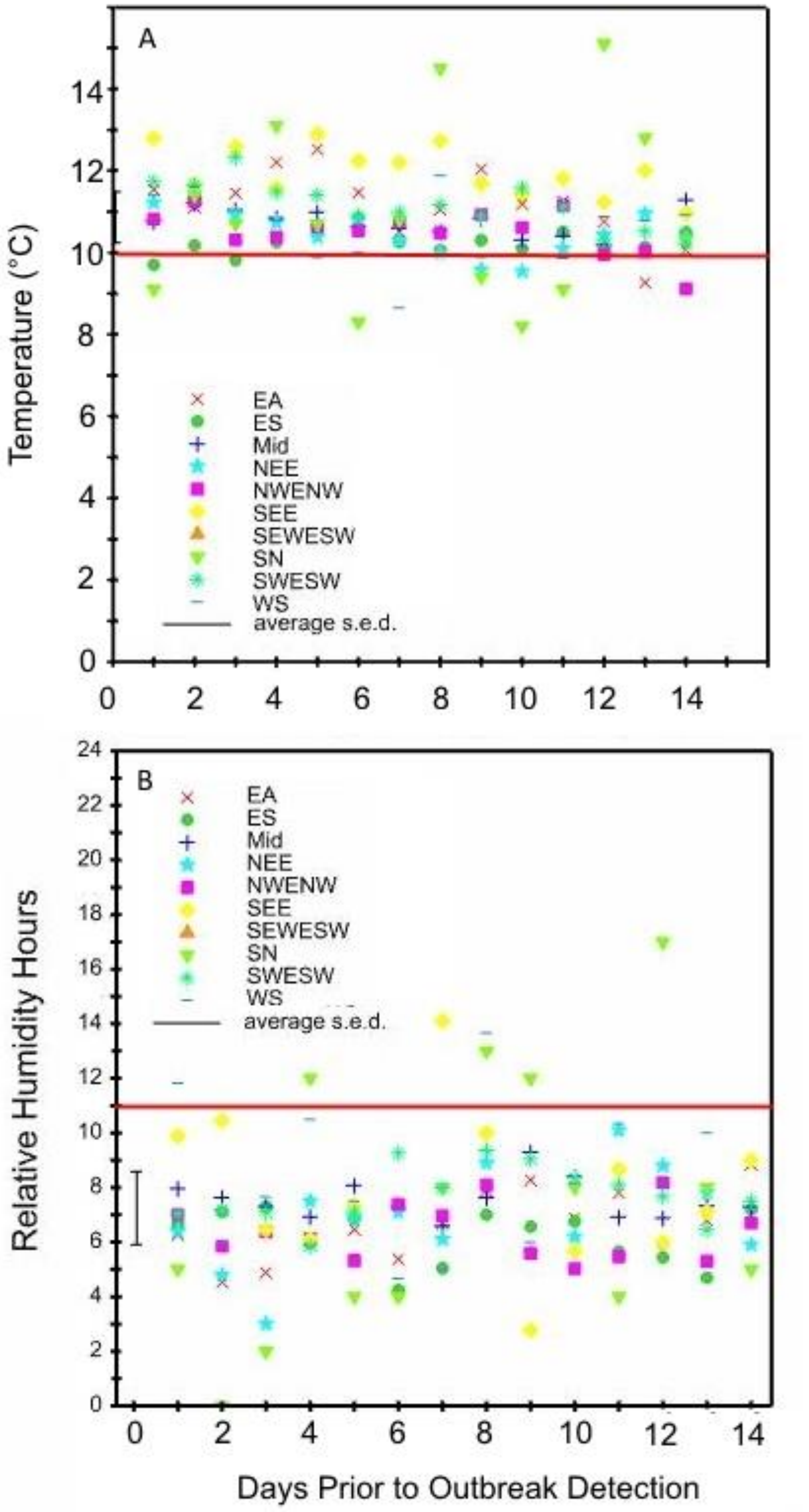
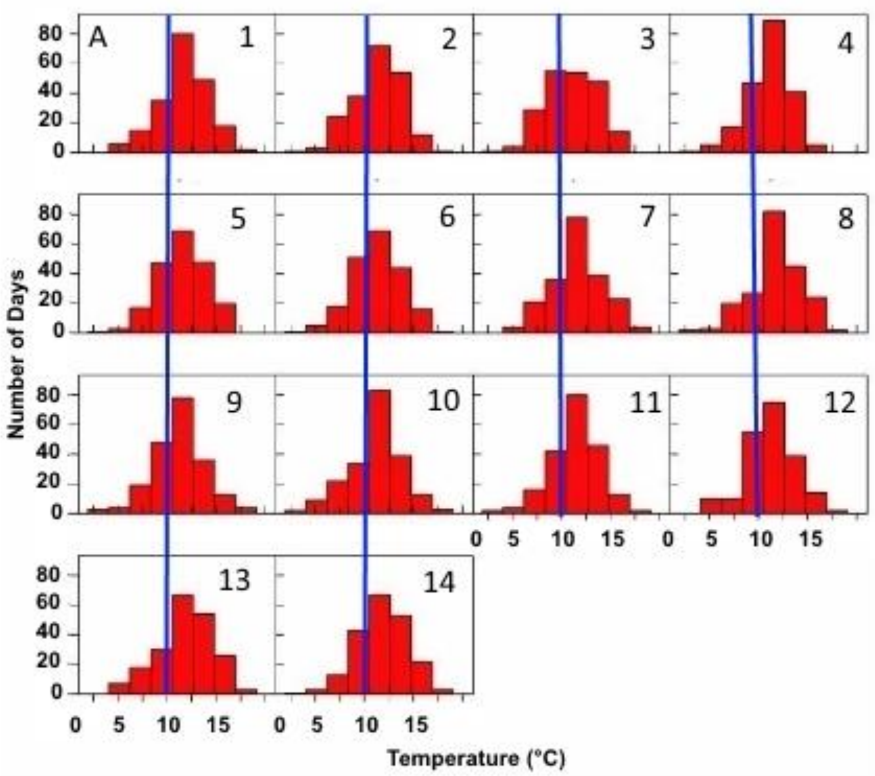


Figure 2.23: The (A) mean minimum temperature and (B) mean duration of relative humidity ≥90% for all climatic districts in 2014 for the 14 days prior to detected outbreak in each region.



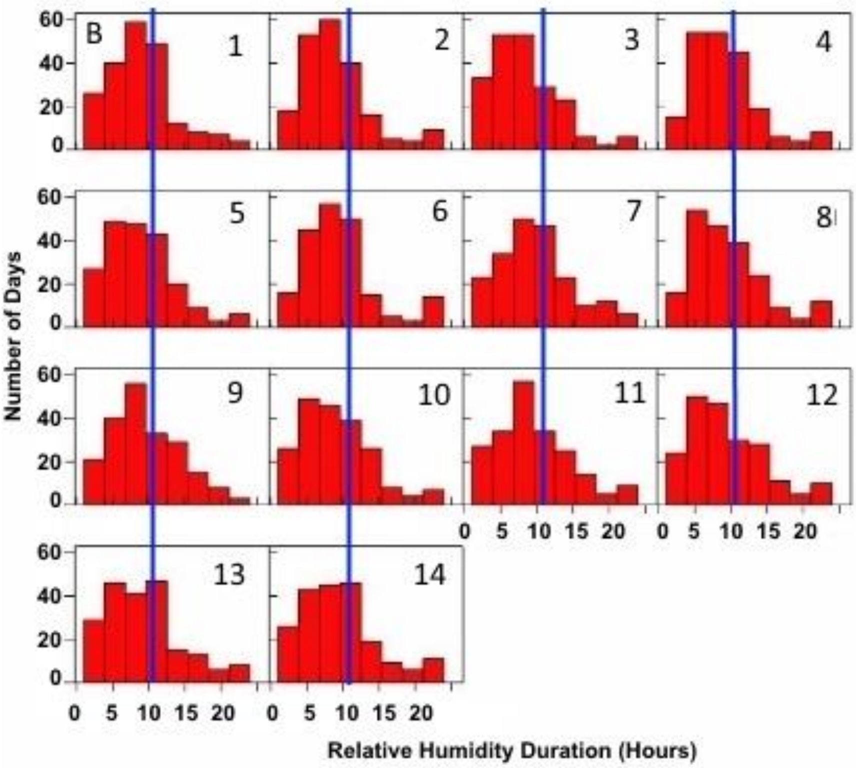


Figure 2.24: The (A) average minimum temperature and (B) duration of relative humidity ≥90% for Midlands for the 14 days prior to detected outbreak in each district (1 = 1 day prior, 2 = 2 day prior, etc.).

2.5 DISCUSSION

Great Britain has very different regional weather patterns; from cool and wet in Scotland, to dry and warm in the Midlands, and warm and wet in the southeast of England. This variation is manifested in different frequencies of Smith Period alerts when mapped (Figures 2.7, 2.8), and disparity in Smith Period performance across the country. The ROC analysis showed that at the national scale the Smith Period can be classified as a 'fair' diagnostic tool. At a regional level, however, it was not performing uniformly across the country or between years. Thus, the first take-home message for the potato industry is that the Smith Period works better in some parts of the country than others.

The correlation between Smith Period alerts and late blight outbreaks was high in some years, e.g. 2012, but low in others, e.g., 2006 and 2010. For example, the Smith Period was shown to work very well in districts such as the southwest of England and southern wales and in many years an AUROC >0.9 was achieved. In 2006, 2013 and 2014 the AUROC values were 0.61, 0.68 and 0.64 respectively. This is despite a high frequency of Smith Period alerts in all those years (Fig. 2.10). This indicates that even with a high frequency of alerts, high risk periods for disease development are being missed. In 2012, a year that was very wet and had a great deal of blight pressure, the Smith Period performed very well across all climatic districts, excluding Scotland North; the AUC's for each region were > 0.9 except for east Anglia which was still high with 0.86. However, in 2007 another wet year with heavy disease pressure, the AUROC values for northwest England and north wales were 0.41 and 0.66 respectively, so even under those conditions, high risk periods of blight were being missed. Thus, the second take-home message for the potato industry is that the Smith Period performs better in some years than others.

The Smith Period was developed in the 1950s to improve upon the previous Beaumont system, which had a 20% failure rate at indicating risk prior to outbreaks. The results of this study reveal a higher failure rate for the Smith Period in most years and districts, which by the same reasoning used by Smith would call upon the potato industry to improve the Smith Period (Figure 2.10). We can speculate that the size of our historical analysis provides more detail regarding the nature of potato late blight outbreaks; Smith conducted his research on ~200 reported outbreaks, whereas >2000 were analysed in this study. It is also likely that Smith Periods were a robust tool in their day, but the current genotypes of *P. infestans* are more aggressive and able to cause infections under conditions outside of the environmental envelope Smith defined for the populations present in the 1950's. Whatever the reasons, we can conclude that there is potential for improvement of the GB national warning system for late blight, which would be our third-take home message for the potato industry.

The question remains as to whether the less than optimal performance of the Smith Period is due to the requirement for two days of conducive conditions of blight as opposed to one, or if the failing is within the actual core environmental criteria or both. The ROC curves constructed for a single day of the Smith Criteria do reveal a significantly improved diagnostic tool (compare Figures 2.17 and 2.18), but there are still districts in certain years with poor performance based on AUROC; east Anglia 2003 (0.73), north east England 2005 (0.56), northwest England and north Wales 2006 (0.3), south east England 2006 (0.5), east Anglia 2006 (0.76) and north east England 2013 (0.55). Furthermore, as expected, the requirement of only a single day of conducive conditions for late blight as opposed to two led to an increase in the frequency of alerts (compare Figures 2.19 and 2.20).

Examination of frequency of alerts relating to stage of outbreak was particularly interesting. The mean frequency of Smith Periods and Smith Criteria was highest prior to severe alerts in all years examined except 2012. This indicates that for the development of severe outbreaks, more warnings are received than smaller scale outbreaks, indicating that for a severe outbreak to occur there is a build-up of inoculum from multiple disease cycles.

Finally, the examination of the mean temperature and relative humidity criteria individually provided very useful results. While 2014 and the Midlands were selected as an example year and district, all other years and districts showed highly similar results. The minimum temperature per day (averaged across all outbreaks) in the 14 days prior to the date outbreaks were reported was almost always well above the 10°C threshold of the Smith Period, and the mean duration of high relative humidity was almost always well below the threshold of 11 hours. This indicates that the requirement for 11 hours of ≥90% RH should be lowered. We hypothesise that the failure rate of the Smith Period could be decreased by widening the environmental envelope of the core criteria in this manner. This is the subject of the following chapter where the envelope of environmental conditions required by the contemporary GB *P. infestans* population is investigated using a series of controlled environment experiments.

It should be noted that although The FAB dataset provided was an excellent resource with which to evaluate the historic performance of the Smith Period across Great Britain, these are survey data and are thus subject to the vagaries and work rate of blight scouts in different areas. Nevertheless, we work under the assumption that this is of little consequence to our analyses, given the high quality of experience of the personnel who collect the data.

2.6 CONCLUSIONS

This study revealed that the overall performance of the Smith Period across Great Britain during the study period was ‘fair,’ with an AUC of 0.686 (95% CI = 0.540–0.832). There was, however, significant variation in performance across the country and between years. Although the Smith Period has served the GB potato industry well as an indicator of high risk conditions for many years, this investigation has shown that there is room for improvement, and we should begin by investigating the temperature and relative humidity requirements for infection in the contemporary pathogen population.

3 CHAPTER THREE: CONTROLLED ENVIRONMENT EXPERIMENTS TO IDENTIFY RISK CRITERIA FOR *PHYTOPHTHORA INFESTANS* INFECTION

3.1 ABSTRACT

Phytophthora infestans is an oomycete pathogen and the causal agent of potato late blight disease. The ability to accurately identify environmental conditions, specifically temperature and relative humidity criteria, which create 'high risk' situations for infection, is crucial when developing decision support tools for growers. The Smith Period defined high risk conditions in Great Britain (GB) for potato late bight development in the 1950s as: two consecutive days where each day the minimum temperature is ≥ 10°C and there are at least 11 hours when the relative humidity is ≥90%. The Fight Against Blight (FAB) campaign has been sampling and monitoring the *P. infestans* populations in GB since 2003, during which time two new genotypes appeared and have come to dominate the population: 6_A1 and 13_A2. For these dominant genotypes the minimum temperature, level of relative humidity and duration of exposure to high relative humidity required for infection is investigated. Experiments were conducted with detached leaves and whole plants of potato cultivar Maris Piper using a gradient plate and growth rooms to control temperature and glycerol-water solutions to control relative humidity. In each case, environmental conditions were monitored with iButton data loggers. The results indicate that the pathogen can cause infection at lower temperatures and lower humidity thresholds than the current Smith Criteria of 10ºC and 90% RH. Infection efficiency and rate of lesion growth, however, drop markedly at below these threshold levels which will reduce the rate of pathogen infection and spread in the field. Conversely a shorter duration of the high humidity resulted in a relatively small reduction in infection efficiency offering potential for a simple but effective change to the current criteria.

3.2 INTRODUCTION

The Smith Period defines a set of temperature and relative humidity criteria that are considered to generate high risk for potato late blight (PLB) development in field crops in Great Britain (GB). If there are two consecutive days where the minimum temperature does not fall below 10°C and there are at least 11 hours of relative humidity ≥ 90% a Smith Period has occurred (Smith, 1956a). This set of criteria was based on that of Beaumont (Beaumont, 1947) and defined in the 1950s. It has not been re-evaluated since, and until 2017 was used by Blightwatch, the Agricultural and Horticultural Development Board, Potatoes Division (AHDB Potatoes) national warning system for potato late blight in GB. Previous analyses (Chapter 2) identified that the Smith Period could be improved as ~20% of reported outbreaks from 2003 – 2014 in each climatic region did not receive alerts in the 28 days prior to outbreak detection with significant variations in performance in the different climatic districts of GB and years.

Relative humidity and temperature criteria that define risk of infection are important features of most decision support tools for late blight (Crosier 1934, Cao, Ruckstuhl & Forrer, 1997, Mizubuti & Fry, 1998, Taylor, Hardwick, Bradshaw & Hall, 2003, Hardwick, 2006). It is from these that more sophisticated tools may be developed but it remains critical that these criteria are correctly defined for the grower to have confidence in the system. The risk criteria of the Smith Period can thus be broken down into three areas for evaluation, (1) the temperature component, (2) level of relative humidity and (3) duration of exposure to each. There are complex interactions between these factors and the pathogen’s response to them. For example, as temperature increases the rate of pathogen growth will increase and shorten the time window required for infection to occur. However, in practice, field humidity levels tend to decrease with increasing temperatures which will impede the infection process. Conversely, at lower temperatures the time required for infection extends but there is often more moisture available.

The Fight Against Blight (FAB) campaign run by AHDB Potatoes, has been monitoring populations of *P. infestans* in GB since 2003, Scouts from across the country take samples from outbreaks that are recorded and genotyped at the James Hutton Institute in Dundee. This continues to provide a great deal of information regarding the current populations of *P. infestans*. We know that since the Smith Period criteria were first developed the populations of *P. infestans* have changed dramatically across the Europe and Great Britain, (Spielman et al., 1991, Dyer et al, 1993, Andrivion, 1996, Day & Shattock, 1997). Two clonal lineages, 6_A1 and 13_A2 emerged around 2005, have displaced other lineages and now dominate the pathogen population (Cooke et al., 2003, Day et al., 2004, Kildea et al., 2003, Cooke et al., 2008, Lees, et al., 2012). It is known that pathogen genotypes may vary in response to environmental variables (Cooke et al., 2012, Mizubuti & Fry, 1988) and there is thus speculation about the aggressiveness and fitness of these isolates and the fact that the Smith Period temperatures and relative humidity criteria may no longer be representative of the contemporary populations of *P. infestans* in the field. There is thus need to re-evaluate these infection criteria using isolates of *P. infestans* representative of current GB populations.

Previous studies have examined the current genotypes of *P. infestans*, to categorize and compare their infection efficiencies, aggressiveness and fitness. A study based on isolates from the early stages of the newly dominant lineages found there was a clear difference in ability to infect at lower temperatures between the 6_A1 and 13_A2 isolates sampled in 2006 (Cooke et al., 2012). Isolates of 13_A2 appeared better adapted at 13°C than at 18°C compared to 6_A1 and this was thought to be a factor driving changes in the frequency of different lineages over time. A subsequent research project (Chapman, 2012) examined over 50 isolates of *P. infestans* with many representatives of the 6_A1 and 13_A2 lineages selected. In this study there was a greater range of responses amongst isolates of a single genotype and no single genotype appeared better adapted. Her analysis and that of others (Hartill, et al., 1990) reported infection occurring at temperatures below 10°C which corroborates information from growers and agronomists who had reported cases of blight infecting below the temperature threshold of the Smith Period. Such observations led to questions about its current relevance and prompted this reappraisal.

In this study, a selection of isolates representing major genotypes in the GB population is used to evaluate the infection criteria for *P. infestans*; through a range of temperatures, relative humidity levels and duration of exposure required for infection.

3.3 MATERIALS AND METHODS

3.3.1 Potato

Seed tubers of the potato cultivar Maris Piper were grown in pots in the glasshouse and detached leaflets of similar aged leaves were harvested from the mid-section of the plants after approximately 6 weeks growth for use in these investigations. Maris Piper was selected as it was the most commonly grown cultivar in Great Britain (16% of the planted area) and the variety on which FAB scouts most frequently detected potato late blight. It is relatively susceptible to PLB, on a resistance scale of 1-9, with 1 being the most susceptible, it scores 4 and 5 for foliar and tuber blight, respectively.

3.3.2 Relative Humidity Chambers

Three different sizes of relative humidity chamber were developed for different experimental needs. Each chamber had an iButton (Maxim Integrated, San Jose, CA) data logger placed inside to record the relative humidity and temperature during the experiment. The target relative humidity levels were 70, 80, 90 and 100%.

3.3.3 Small relative humidity chambers

Small relative humidity chambers were made from square petri dishes (10 x 10 x 1.5cm), with 25ml of a glycerol-water solution to achieve the desired relative humidity. A stiff square plastic mesh slightly smaller than the base supported detached leaflets so that they would not touch the glycerol-water solution. Four detached leaflets were placed in each chamber and each inoculated with four 5µl droplets. The dishes were then sealed with Parafilm and placed on a temperature gradient plate (Grant Instruments, Cambridge, UK). This comprised an enclosed chamber with an aluminium base with integral cooling and heating units installed in opposite sides to create a controlled and programmable temperature gradient. After the desired exposure period in the sealed chamber with the glycerol-water solution the plastic mesh containing the inoculated leaflets was transferred to a new dish base with 25ml of water to achieve 100%RH, resealed and transferred back to the gradient plate. This process effectively maintained the detached leaflets for at least seven days to allow for infection efficiency to be scored.

3.3.4 Medium relative humidity chambers

Medium relative humidity chambers (38x16x9cm) were made from clear hard plastic storage boxes with 300 ml of a glycerol-water solution placed in the bottom to achieve the desired relative humidity and a stiff square plastic mesh slightly smaller than the base onto which the detached leaflets were placed for inoculation. Each chamber held 18 – 24 detached leaflets. Once leaflets were inoculated and placed into the chamber, it was wrapped inside a large clear plastic bag. The chamber was then placed inside a large growth room with no light or window and set to a desired temperature. After the desired exposure time, the leaflets were removed from the chamber and transferred to another chamber of the same size with moist tissue paper to achieve a 100% RH environment, wrapped inside a large clear plastic bag and placed in a north-facing cooled glasshouse to incubate and allow lesion development.

3.3.5 Large relative humidity chambers

Large humidity chambers (69x42x74cm) were made from large hard plastic storage boxes with 1200ml of glycerol-water solution placed in a smaller flatter box on the base of the chamber covered with a hard-plastic mesh lid, on which to place whole plants for exposure to the desired relative humidity. Plants were not watered the day before they were placed into the chamber for inoculation, and their pots were sealed in plastic bags to limit the amount of extra water introduced into the environment. The chambers were kept in large dark windowless growth rooms that were temperature controlled. After exposure for the specified duration each plant was removed from its chamber, the plastic bag around the pot removed and the plants were incubated on the bench in a north-facing glasshouse in ambient relative humidities.

3.3.6 Glycerol standardization to achieve specific relative humidity

Glycerol has been identified previously as being able to adjust the relative humidity in small enclosed chambers (Johnson, 1940, Forney & Brandl,1992, Li et al., 2014). Glycerol solutions of 0, 20, 30, 40, 60, 70 and 80% by volume in water were mixed and 25, 300 and 1200ml volumes were added to the small, medium and large relative humidity chambers respectively. These were tested at 10°C in the medium and large chambers and at six different temperatures (between 6 - 15°C) in the small chambers. During testing, detached leaflets or whole plants were also placed in the chambers with iButtons to monitor temperature and humidity. Each concentration, 0, 20, 30, 40, 60, 70 and 80% was tested in each chamber at least eight times. The resultant data were fitted to a general Gaussian model in MATLAB for each chamber size where, *x* is the glycerol concentration where A is the height of the curves peak, B is the position of the centre of the peak and C is the width of the bell curve:

$$\mathrm{f(x)} = \mathrm{A} * \exp(-\left(\frac{\mathrm{x-B}}{\mathrm{C}}\right)^2) \qquad (1)$$

3.3.7 Phytophthora infestans *isolates*

Eight isolates of *P. infestans* were selected from FAB outbreaks sampled in 2012 or 2013 and stored at the James Hutton Institute, Dundee. Three 6_A1 isolates (6_A1_11022B, 6_A1_110742, 6_A1-8_9467A), three 13_A2 isolates (13_A2_1_9922C, 13_A2_2_10318, 13_A2_5_10014D), one 7_A1 isolate (7_A1_10290) and one 8_A1 isolate (8_A1_10702B) were used.

3.3.8 Phytophthora infestans isolate maintenance and preparation

Isolates were maintained throughout all experiments on detached Maris Piper leaflets in clear plastic boxes lined with moist paper towels, sealed in clear plastic bags and kept in a north-facing glasshouse. Each week sporangia were collected by washing a sporulating lesion in a beaker of water and then placing the beaker in the fridge for several hours to promote zoospore release. Droplets of zoospore suspension were pipetted onto fresh Maris Piper leaflets. Post-inoculation the boxes were kept in the dark for 24 hours and then exposed to the light and incubated in the north-facing glasshouse for a week before repeating the process. Sporangia for experimental use were harvested from these leaflets by rinsing leaflets gently into a beaker of water. The concentration of inoculum to be used in each trial was standardised by counting sporangia using a haemocytometer. A concentration of 1000 spore/ml was the standard used unless specified otherwise. Inoculum used in experiments was not chilled before use to limit zoospore release. Infection efficiency was calculated for all experiments as the number of percentage of droplets/inoculations which lead to observable infection of the leaf.

3.3.9 Droplet Size, Inoculum Concentration and Isolate Screening

Initial experiments were conducted to investigate the importance of droplet size, inoculum concentration, leaf wetness and establishment of the infection efficiency of the selected isolates. A droplet size that would 'hang' on a leaf was important to define for use in the whole-plant experiments and was used throughout all experiments for consistency. The importance of a droplet which can 'hang' also corresponds to the size of droplet or dew drop that would be found on plants in the field. Larger droplets would be more prone to dripping off the leaf due to gravity. The size of droplet used in all inoculations was 5µl, unless specified otherwise. The length of time it took a 5µl droplet to evaporate was examined at various levels of relative humidity to understand how this influenced infection rate. Within a droplet there is clearly a 100% saturation and a large droplet that takes longer to evaporate would thus have greater infection rates even in lower relative humidity environments as it would take longer to dry. Further tests on infection efficiency (IE) for a larger 20µl droplet compared with the 5µl droplet were conducted. In addition, the IE of inoculum at a concentration of 1000 versus 5000 spores per ml was examined. These preliminary tests were completed using all eight of the selected *P. infestans* isolates. This allowed for characterization of IE to select the most suitable isolates for further experiments that were constrained to fewer than eight isolates.

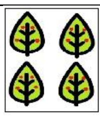
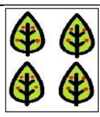
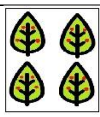
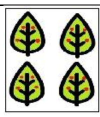
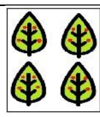
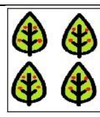
3.3.10 Gradient Plate Experiments

Infection efficiencies of two isolates, one 6_A1 and one 13_A2 were examined using the small relative humidity chambers on the temperature gradient plate arranged in a 7 x 6 layout; six columns of seven chambers, each column representing a different temperature in the gradient from 6 - 15°C (Figure 3.1). Each chamber contained 25ml of a glycerol-water solution to achieve either a 70, 80, 90 or 100% relative humidity (concentration as determined above). On the hard-plastic mesh within each chamber there were 4 Maris Piper leaflets, two of which were inoculated with four 5µl drops of the 6_A1 inoculum and two were inoculated with four 5µl drops of the 13_A2 inoculum. An inoculum concentration of 1000 spores/ml was used in each case. Post inoculation the chambers were sealed for durations of 6, 11 or 24 hours, after which the glycerol solution was replaced with water to maintain leaflet integrity and the chambers were resealed. The combination of isolates (2), humidity levels (4), durations (3) and temperatures (6) resulted in 144 treatment combinations. The scale of the study necessitated the use of a randomized split-plot design spread over 4 gradient plate runs, each of which took a minimum of 7 days to run. An additional 24 positive control treatments (100% humidity treatment) were allocated in each column across the design. This resulted in a complete set of 168 leaves for the experiment. The experiment was completed twice in entirety using different isolates of 6_A1 and 13_A2 each time. The leaflets were photographed 3, 5 and 7 days after exposure with a scale bar. They were scored for lesion development and lesion size was measured using Image J software (Schneider, Rasband & Eliceriri, 2012).

Results were analysed for overall IE using binary logistic regression to determine significance of factors, the total infected (1) versus not infected (0) for each variable combination, a Walds statistic was also used for indicating which terms should be dropped from the model. Polynomial surfaces were fitted to the data in MATLAB:

$$f(x, y) = A + B * x + C * y + D * x^2 + E * x * y \tag{2}$$

with least absolute residuals corrections, where *x* is days post inoculation and *y* is temperature. Summary statistics comparing lesion sizes were also conducted with ANOVA analysis in GenStat to assess variation.

Column 1	Column 2	Column 3	Column 4	Column 5	Column 6
					

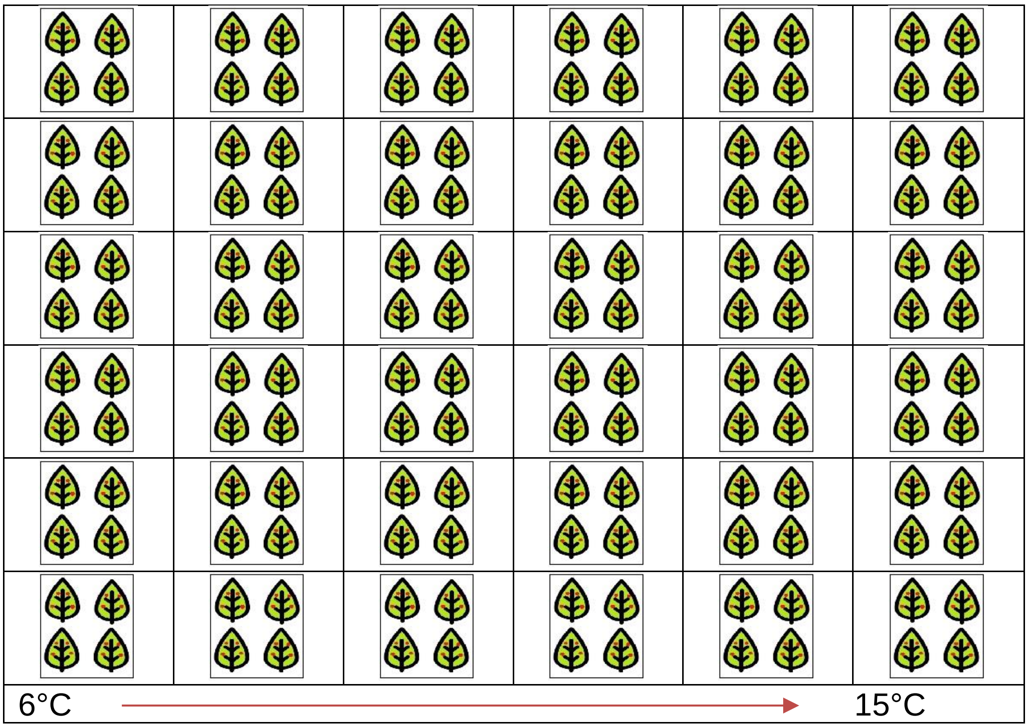


Figure 3.1: Gradient plate experiment layout, four leaflets per small relative humidity chamber with seven chambers per column. The split plot design is made up of four randomized plate layouts in which chambers for 70, 80, 90 and 100% relative humidity and exposure durations of 6, 11 and 24 are randomized across all four plates.

The detached leaflet experiments on the gradient plate allowed for accurate control of temperature and relative humidity and the ability to test many variables simultaneously.

3.3.11 Whole Plant Experiments

The use of whole plants in larger chambers restricts the ability to test the same number of variables and replicates as the gradient plate but allows verification of results found on detached leaflets. Whole plants also do not need be kept in high relative humidity environments post-exposure and thus provide a better system for investigating factors such as length of exposures to high relative humidity. Large chambers were used to achieve targets of 80, 90 and 100% relative humidity. Twelve chambers were used for each run of the experiment, four for each relative humidity to be tested. The effect of duration of exposure was investigated, looking at durations of 0, 4, 6, 8, 12, 16, 20 and 24 hours. Plants were inoculated and placed into their respective humidity chamber for the specified duration before being placed in the north-facing glasshouse. Four replicates were tested at each relative humidity for each duration of exposure. The positions of the plants within each chamber were randomized as were the positions of the chambers within the larger growth room. One isolate each of the 6_A1 and 13_A2 genotypes, used previously within the gradient plate experiments were used. Prior to the day of each experiment, ten leaflets on each plant were marked with pink tape for 6_A1 and ten leaflets were marked with blue tape for 13_A2. Each marked leaflet was inoculated on the underside with two 5µl droplets of 1000 spores/ml inoculum, one on either side of the mid rib. The plants were scored seven days post inoculation for lesions. The experiment was repeated at 5 different temperatures; 7, 10, 14, 18 and 21°C.

The binary infection efficiency data was processed in MATLAB and fitted using generalized linear model regression for each relative humidity level, using the glmfit MATLAB tool and the binomial and probit parameters. A two-polynomial curve (2) where x is relative humidity and y is duration was fitted to the resultant glm regression data.

3.4 RESULTS

3.4.1 Glycerol Standardization

Glycerol was effective at adjusting relative humidity levels in a predictable manner in all three experimental systems. The Gaussian curves fitted to the iButton data from the glycerol concentration standards for the small, medium and large relative humidity chambers, all had r^2 values all greater than 0.92 (Figure 3.2). The variables A, B and C for each curve are shown in Table 3.1. The medium and large relative humidity chambers were tested at 10°C while the small relative humidity chambers on the gradient plate were tested at six temperatures between 6 - 15°C and showed no significant variation. The performance of the small and medium chambers was almost identical but higher glycerol concentrations were needed to achieve the same humidity levels in the larger chamber that contained transpiring plants. In subsequent experiments the target relative humidity was achieved with glycerol concentrations derived from this test.

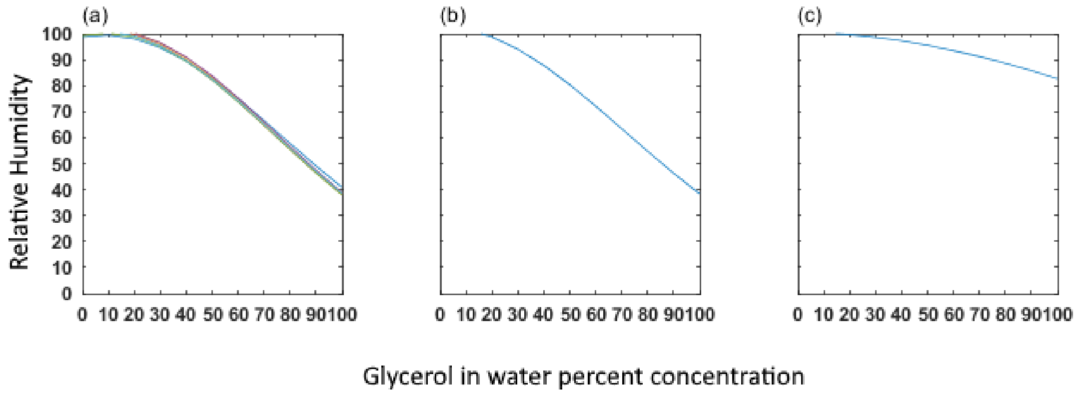


Figure 3.2: Glycerol standardization curves fitted with a general Gaussian model indicating the relationship between concentration of glycerol and relative humidity in (a) small (25ml), (b) medium (300ml) and (c) large (1200ml) chambers. Model parameters specified in Table 3.1. Curves for different temperatures shown in a).

Table 3.1: Variables for the general Gaussian models to determine glycerol concentration for desired relative humidity level

	A	B	C
Large Chambers	100.60	-2.34	231.30
Medium Chambers	102.70	0.16	100.60
Small Chambers (6.16°C)	99.46	8.46	97.08
Small Chambers (8.49°C)	101.70	6.80	94.20
Small Chambers (10.34°C)	102.00	7.75	93.72
Small Chambers (12.10°C)	101.40	9.68	92.15
Small Chambers (13.82°C)	100.20	8.71	92.37
Small Chambers (15.28°C)	100.80	7.76	94.17

3.4.2 Droplet Size, Inoculum Concentration and Isolate Screening

Prior to running leaf infection studies, the rate of evaporation of 5µl droplets of water from leaf surfaces at relative humidity levels of 50 – 100% were examined. It was found that with *n* = 48 droplets tested at each relative humidity there were clearly defined points when droplets had evaporated completely. After 6 hours exposure no droplets were left in environments of <85% RH while 90 – 100% of droplets remained after six hours of exposure in environments of 90 – 100% RH.

Initial screening of IE at 10°C and 80, 90 or 100% RH for 11 hours for all eight isolates was completed using the medium sized relative humidity chambers and a randomized split-plot design across three boxes for each RH (Figure 3.3). All isolates infected at 100% RH but the infection efficiency varied from a mean of below 60 to 100%. There was a noticeable reduction in infection rates at 80% RH, though isolate 13_A2_2_10318 showed significantly more infection at this lower humidity than the other isolates, indicating that this is an isolate to be examined in more detail. An examination of the variation between and among genotypes did not indicate any clear effect of genotype on IE at any level of relative humidity.

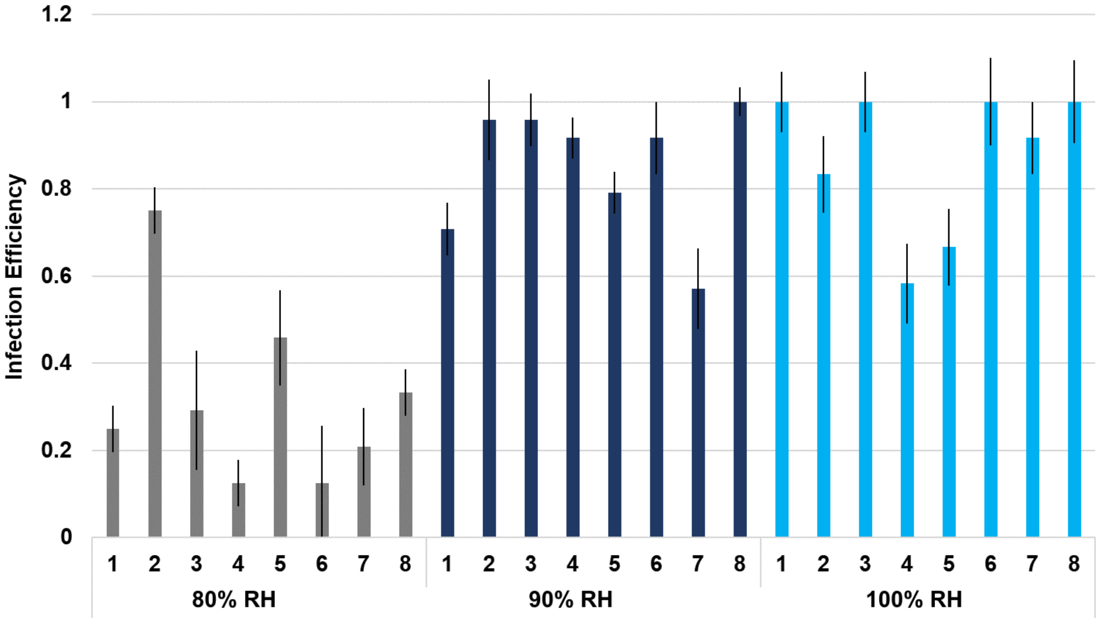


Figure 3.3: Infection efficiency at 80, 90 and 100% RH for 11 hours at 10°C for eight different isolates: (1) 13_A2_1_9922C, (2) 13_A2_2_10318, (3) 13_A2_5_10014, (4) 6_A1_11022, (5) 6_A1_11022, (6) 6_A1_8_9467, (7) 7_A1_10290 and (8) 8_A1_10702B.

A second initial screening of IE with eleven-hour duration exposures to 80% RH at 6°C for all eight isolates was carried out (Figure 3.4). We used these conditions as they are not optimum conditions and our standard inoculation of 5µl droplets with 1000 spores per/ml concentration showed lower IE rates than in more ideal conditions with higher relative humidity levels and temperatures. IE of the eight isolates using 20µl droplets of 1000 spores per/ml inoculum and 5µl droplets of 5000 spores per/ml inoculum were assessed. Figure 3.4 shows that both the larger droplet size and increased inoculum concentration caused increases in IE; however, the larger droplet size showed the highest increase across all eight isolates. The larger droplets take longer to evaporate so the inoculum within the droplet is in a prime high relative humidity environment for longer even though the free air around the droplet is of lower relative humidity. Interestingly we see again that the isolate 13_A2_2_10318 showed the highest overall infection rates in the lower temperature and relative humidity conditions compared to the other seven isolates.

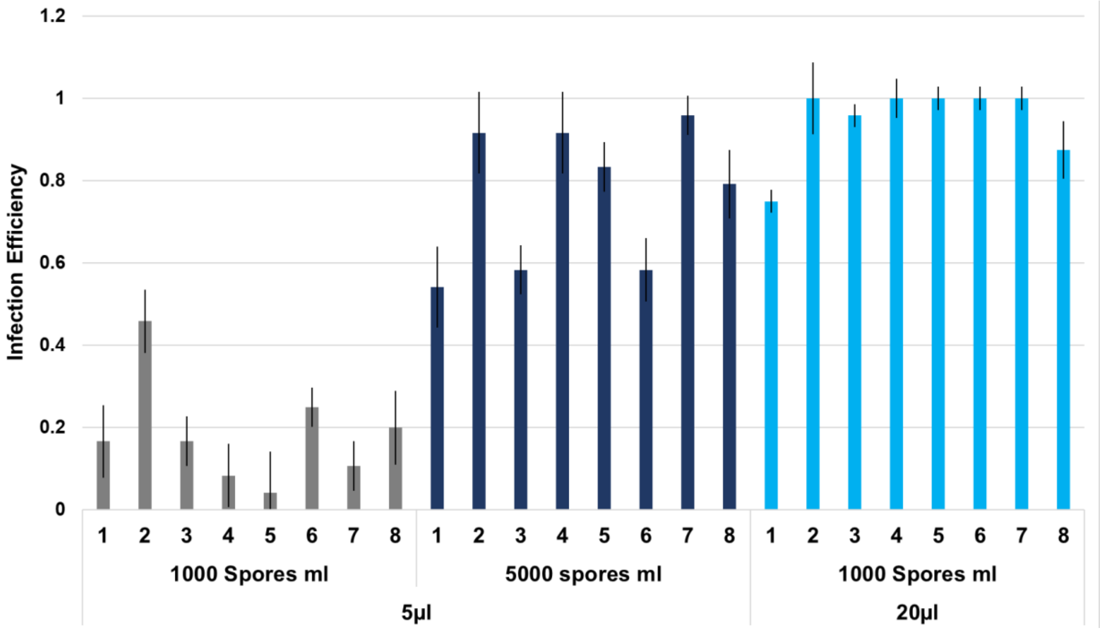


Figure 3.4: Infection efficiency of 11 hours at 6°C in 80% RH for eight different isolates: (1) 13_A2_1_9922C, (2) 13_A2_2_10318, (3) 13_A2_5_10014, (4) 6_A1_11022, (5) 6_A1_11022, (6) 6_A1_8_9467, (7) 7_A1_10290 and (8) 8_A1_10702B two different droplet sizes 5 and 20µl and 1000 and 5000 spores per ml inoculum concentrations.

3.4.3 Gradient Plate Experiments

The gradient plate experiment was conducted twice, each including two different isolates of 6_A1 and 13_A2. There was a significant difference in IE [F (1, 89) = 5.716, p = .016] between the two runs of the experiment. The differences between the duration of exposure were significant [F (2, 89) = 5.19, p = .006] but not in combination with other factors, Humidity by Duration by Isolate: [F (18, 89) = p = .35, 0.994]. The factors humidity [F (3, 89) = 333.5, p <0.001], temperature [F (5,89) = 293.66, p = <0.001] and isolate [F (2, 89) = 21.32, p <0.001] were all highly significant in terms of explaining variation in IE. No significant differences between the two 13_A2 isolates were observed [F (1,141) = 0.3, p = .583] but the 6_A1 isolates did differ in IE which potentially explains the significant difference between the two experiments.

Control of the duration of exposure to set humidity levels for 6, 11, and 24 hours proved difficult as there was a need to return the treatments to 100% humidity after the exposure period. Exposure of detached leaflets to low humidity beyond 24 hours desiccates the leaves which would inhibit the ability to accurately detect or assess for infection. For this reason, the data for 6, 11 and 24-hour duration treatments were combined for the polynomial curve calculation of the mean IE data. The mean data were fitted for the two 13_A2 isolates and the 6_A1 isolates at 70, 80, 90 and 100% RH (Figures 3.5 and 3.6 respectively with Tables 3.2 and 3.3 summarizing parameter and goodness of fit). The models were normalized to x mean 11.03 and std. 3.11 and y mean 3.75 and std. 2.59. At 70 and 80% RH the IE is extremely low, especially at the lower temperatures. Only at 90 to 100% RH do IE levels increase markedly. The 13_A2 and 6_A1 isolate data are plotted separately but there are no clear differences between their surface plots.

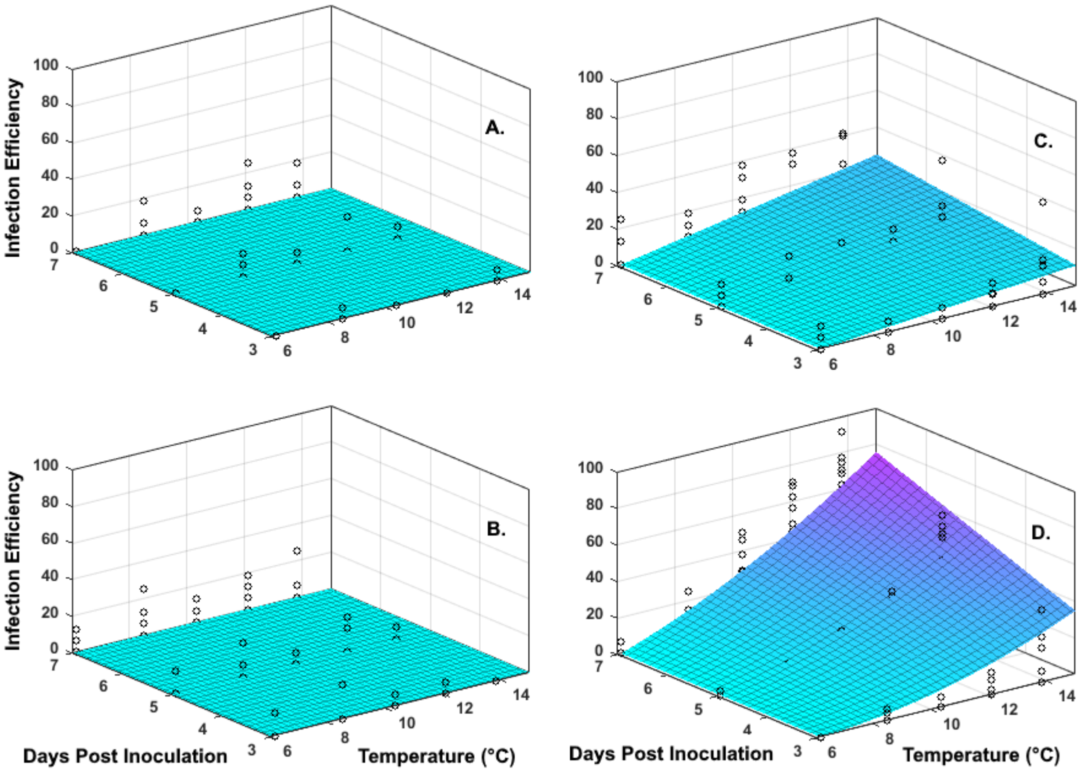


Figure 3.5: Infection efficiency surface plots fit using two polynomial curves for two 13_A2 isolates at (A) 70% RH, (B) 80% RH, (C) 90% RH and (D) 100% RH. Model parameters and goodness of fit found in Table 3.2 and 3.3.

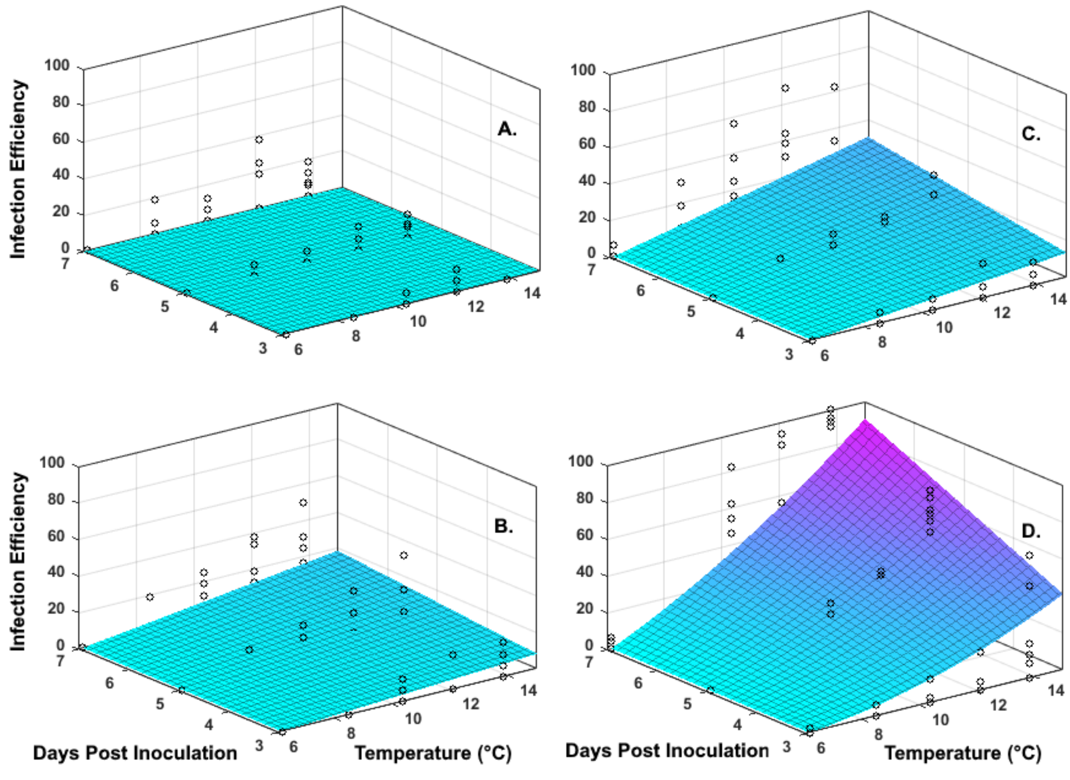


Figure 3.6: Infection efficiency surface plots fit using two polynomial curves for two 6_A1 isolates at (A) 70% RH, (B) 80% RH, (C) 90% RH and (D) 100% RH. Model parameters and goodness of fit found in Table 3.2 and 3.3.

Table 3.2: Model parameters for gradient plate infection efficiency results for relative humidity (RH) and genotypes (GT) of Phytophthora infestans two polynomial curve models fit with gradient plate experimental data

		Parameters with 95% CI									
RH	GT	A	A (CI)	B	B (CI)	C	C (CI)	D	D (DI)	E	E (CI)
70	13_A2	+9.5353e-12	(-0.4289, 0.4289)	1.374e-11	(-0.2889, 0.2889)	1.135e-11	(-0.2827, 0.2827)	4.887e-12	(-0.3256, 0.3256)	7.245e-12	(-0.2837, 0.2837)
70	6_A1	2.306e-05	(-0.6426, 0.6427)	1.473e-05	(-0.433, 0.433)	1.596e-05	(-0.4237, 0.4237)	5.162e-09	(-0.4879, 0.4879)	1.019e-05	(-0.4252, 0.4252)
80	13_A2	0.0007123	(-0.5532, 0.5547)	0.0004548	(-0.3728, 0.3737)	0.000493	(-0.3647, 0.3657)	1.36e-08	(-0.4206, 0.4206)	0.0003147	(-0.3662, 0.3668)
80	6_A1	5.564	(4.733, 6.395)	3.552	(2.992, 4.112)	3.851	(3.303, 4.399)	4.203e-10	(-0.631, 0.631)	2.458	(1.908, 3.008)
90	13_A2	7.436	(6.579, 8.294)	4.77	(4.193, 5.347)	5.167	(4.601, 5.733)	7.671e-16	(-0.6506, 0.6506)	3.314	(2.746, 3.882)
90	6_A1	9.107	(7.925, 10.29)0	5.818	(5.021, 6.614)	6.304	(5.525, 7.083)	0.002234	(-0.895, 0.8994)	4.025	(3.243, 4.807)
100	13_A2	16.45	(15.33, 17.58)	15.9	(15.15, 16.66)	14.74	(13.99,15.48)	3.449	(2.595, 4.303)	9.408	(8.664,10.15)
100	6_A1	20.89	(19.53, 22.24)	18.67	(17.75, 19.58)	17.76	(16.87, 18.65)	3.403	(2.377, 4.43)	11.34	(10.44, 12.23)

Table 3.3: Goodness of fit data for two-polynomial models fit to gradient plate experimental data based on relative humidity (RH) and genotype of *Phytophthora infestans*

		Goodness of Fit:			
RH	GT	R^2	SSE	Adj. R^2	RMSE
70	13_A2	0.8813	406.5	0.8779	1.71
70	6_A1	0.8878	912.7	0.8846	2.562
80	13_A2	0.8805	678.2	0.877	2.209
80	6_A1	0.9213	1527	0.919	3.314
90	13_A2	0.9272	1607	0.925	3.412
90	6_A1	0.9323	3086	0.9304	4.712
100	13_A2	0.9744	2795	0.9737	4.484
100	6_A1	0.9753	4041	0.9746	5.392

Each leaflet was scored and photographed for infection at 0, 3, 5 and 7 days post inoculation with a scale bar and the lesion area for each leaf was calculated with Image J software. ANOVA results for analysis of lesion size correlated with the IE results, duration was just significant [$F(2,90) = 3.16$, $p = .042$], while differences relating to humidity [$F(3,90) = 101.15$, $p < 0.001$] temperature [$F(5,90) = 151.05$, $p < 0.001$] and isolate [$F(2,90) = 5.81$, $p = .003$] treatments were highly significant. Interestingly there was no significant difference between the two isolates of each genotype used but 6_A1 lesions were significantly larger than the 13_A2 lesions (Figure 3.7). Infection at ≤10°C was minimal as was infection below 90% RH.

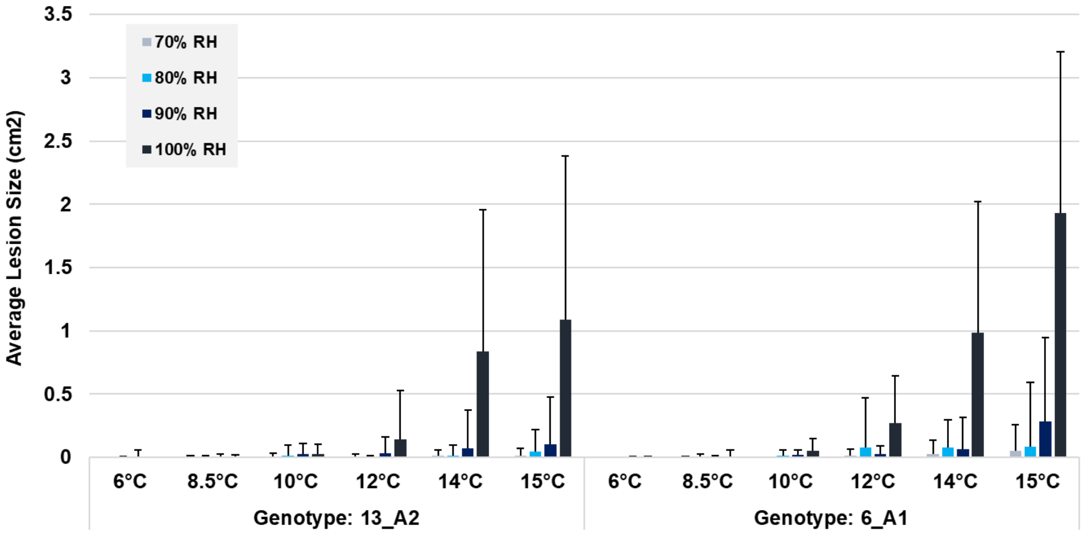


Figure 3.7: Average lesion area of 6_A1 and 13_A2 genotypes at 70, 80, 90 and 100% RH. * supplementary data Table 3 contains regression model predictions for lesion size for each of the four isolates at each temperature.

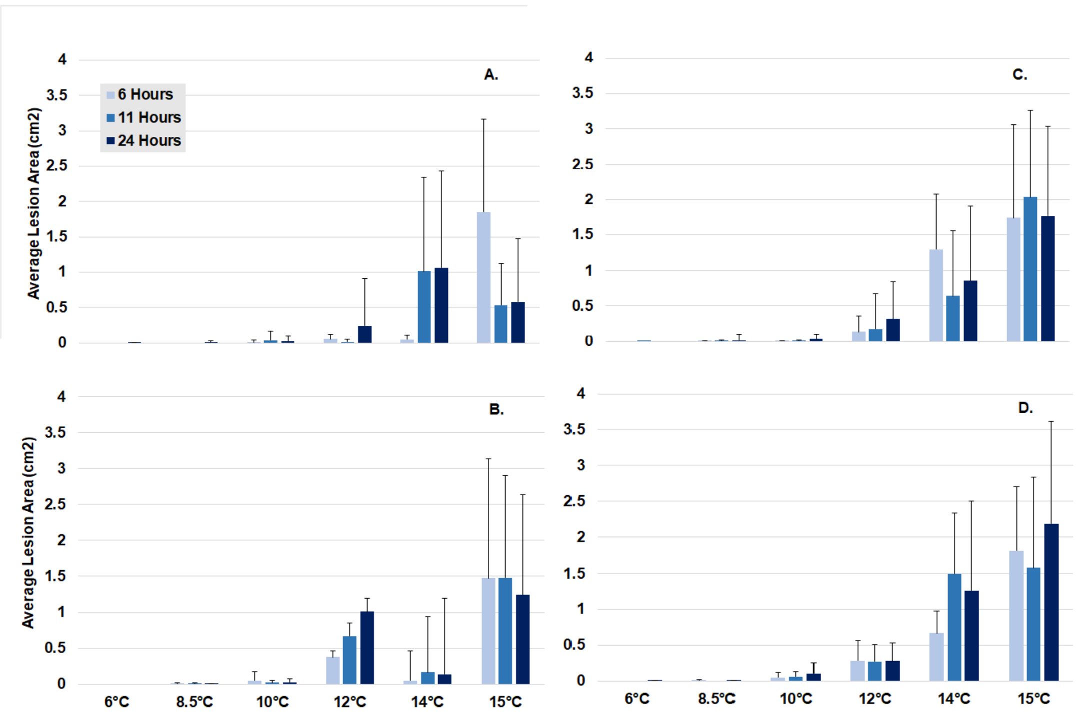


Figure 3.8: Average lesion areas from 6, 11 and 24-hour duration exposures to 100% RH on the gradient plate experiments. (A) 13_A2 isolate one, (B) 13_A2 isolate two, (C) 6_A1 isolate one, (D) 6_A1 isolate two.

3.4.4 Whole Plant Experiments

The large humidity chambers were utilized for a whole-plant experiment to confirm results found using the detached leaf method but also to investigate more thoroughly the duration of exposure to different RH levels required for infection. A RH of 100% is straightforward to achieve with large amounts of water placed into the chamber. The lower 80% level of RH was also achieved as 100% glycerol was required. It proved more challenging to maintain intermediate relative humidity levels and the data set for 90% RH is incomplete due to failed runs which could not be repeated. The mean RH of the completed 90% experiments was 88.89% with std. dev. of 6.56 and 95% CI of 3.03. The mean RH achieved for the 80% chambers was 82% with std. dev. of 3.39 and 95% CI of 1.66. The criteria for judging success of an experiment was whether infection occurred or not. The level of RH and duration of exposure were highly significant factors to explain the variation found (Figure 3.9). The replicate [F (3,696) = 2.78, p = .040] and isolate [F (1,696) = 4.31, p = .038] used did not show a high level of statistical significance. The generalized linear model regression for each RH level is plotted (Figure 3.10). They show that at 100% RH there are significant levels of infection below the 11-hour duration at ≥90%RH threshold defined in the Smith Period. A clear gradient in IE over time is observed at each of the three relative humidity levels. The surface plot of the data indicates a stepwise increase in IE with duration of exposure and RH level, IE remains high despite reductions in the duration of high humidity exposure from the currently adopted 11-hour Smith Period threshold.

Unexpectedly, the effect of temperature did not prove to be a statistically significant factor in this analysis. This may relate to the difficulty in temperature control during the frequent and lengthy process of entering the room to sample the plants.

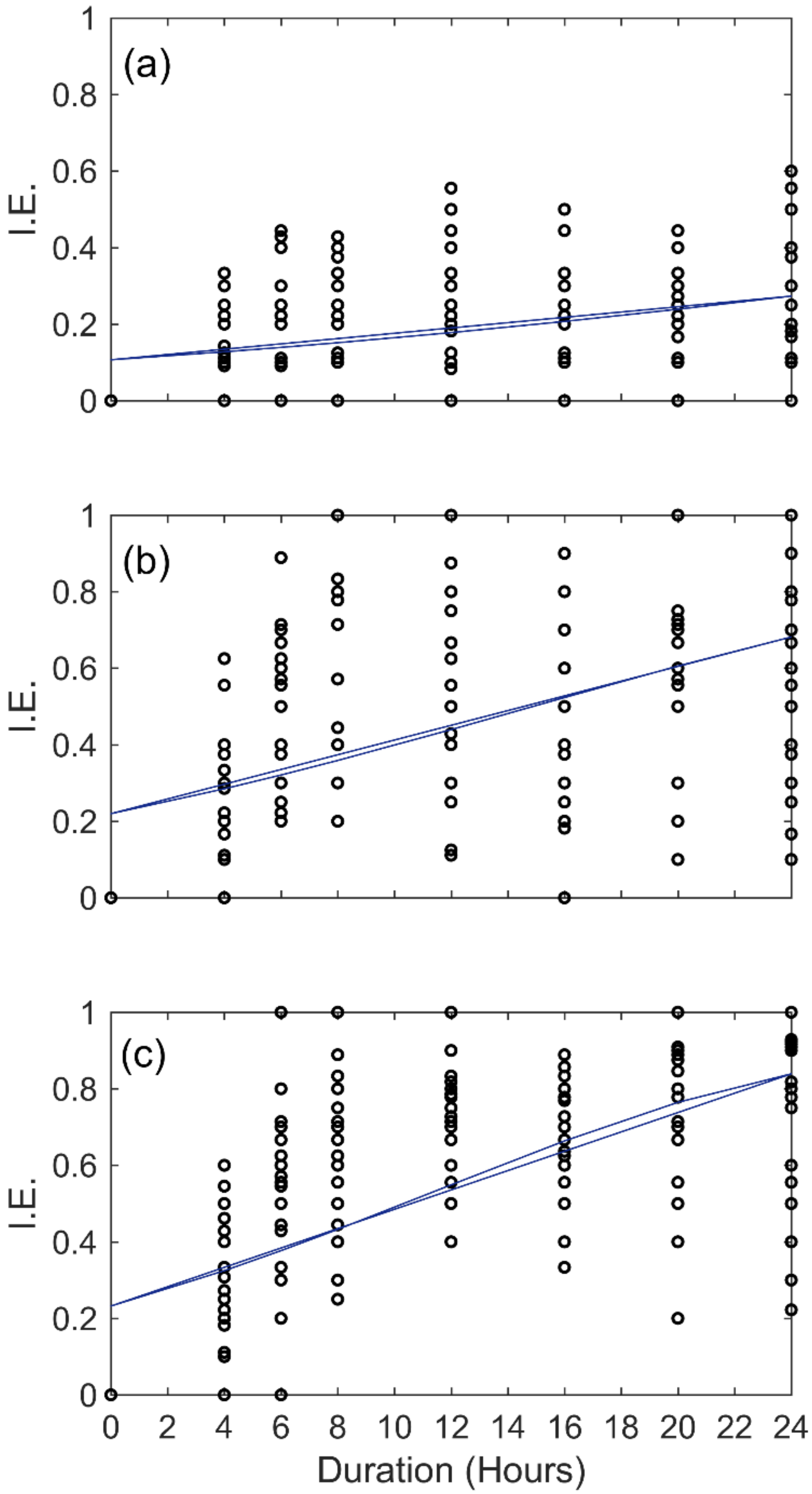


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Figure 3.9: Whole plant infection efficiency rate for (A) 80%, (B) 90% and (C) 100% with generalized linear model regression, summary statistics provided in Table 3.4.

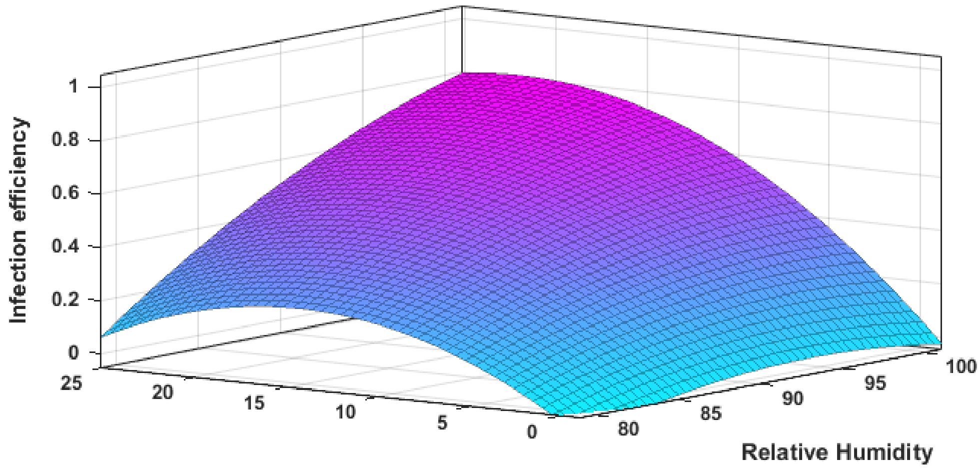

Figure 3.10: Whole plant infection efficiency model of a linear two polynomial for 80, 90 and 100% RH exposures, f(x,y) = A+B*x+C*y+D*x^2+E*x*y+F*y^2, [A = 0.5193 (0.4895, 0.5487), B = 0.157 (0.1444, 0.1696), C = 0.1641(0.151, 0.1771), D = -0.05177(-0.07401,-0.02953), E = 0.07479(0.06214,0.08745), F = -0.09444(-0.1088,-0.08006). SSE: 19.88, r^2:0.6628, Adj. r^2= 0.6604, RMSE: 0.1696.

Table 3.4: Summary statistics for generalized linear model fit to infection efficiency rates of whole plant experimental data at 100, 90 and 80% RH

RH	Coef. Est. b		DFE	Est. Disp. Parameter	Est. Co–Var. Matrix for b		Std. err. Coef.est. b		Corr. Matrix for b		T stat. for B		P values for B	
100	0.745	0	262	1.447	0.002	0.000	0.048	0.004	1.000	-0.830	-15.669	20.412	0.000	0.000
					0.000	0.000			-0.830	1.000				
90	-0.776	0.052	168	1.512	0.004	0.000	0.062	0.004	1.000	-0.837	-12.509	11.619	0.000	0.000
					0.000	0.000			-0.837	1.000				
80	-1.244	0.027	261	1.047	0.003	0.000	0.058	0.004	1.000	-0.858	-21.526	6.883	0.000	0.000
					0.000	0.000			-0.858	1.000				

3.5 DISCUSSION

In this work, aspects of the response of contemporary isolates of *P. infestans* to temperature and humidity criteria that are crucial to late blight decision support systems have been re-examined. Experiments studying the effect of relative humidity, temperature and the duration of exposure have shown that the pathogen is able to cause infection at lower temperatures and lower humidity thresholds than the current Smith Criteria of 10^{o}C and 11 hours of ≥90% RH, respectively. Infection efficiency and rate of lesion growth, however, drop markedly below these threshold levels which would result in dramatic slowing of the rate of pathogen infection and spread in the field. Conversely, a shorter duration of the existing criteria resulted in a relatively small reduction in infection efficiency offering the potential for a relatively simple but effective change to the current Smith Period criteria.

In preliminary investigations the potential of glycerol solutions to manipulate RH levels in incubation chambers was explored. Other work has indicated its potential use in studies of plant pathogen infection processes (Li et al., 2014, Tooley & Browning, 2016). It offers a relatively easy method to control RH, a factor which has previously required the use of complicated apparatus to control (Fry & Minogue, 1981, Forney & Brandl,1992, Harrison 1992). In this study the glycerol concentrations required to control humidity in three chamber sizes with plant material were determined and used in further investigations and may provide reference points for those wishing to conduct similar studies. The limitations found with this method were for the largest chamber size used. The control of relative humidity in a chamber with living plants is difficult; the introduction of soil which holds moisture and plants of various sizes which transpire and introduce moisture into the environment can affect the achievement of the desired RH.

Humidity is a component of most potato late blight decision support systems, with many systems citing the need for 90% RH to induce infection. Periods of low RH have been investigated and shown to reduce sporangia viability (Crosier, 1934, Fry & Minogue, 1981) but the careful control of RH and its impact on IE has not been reported previously for *P. infestans*. This may relate to the difficulty of maintaining and measuring RH under controlled conditions and the complex interactions with other factors such as temperature, air flow and canopy density under field conditions (Harrison, 1992). The impact of RH on IE can be related to leaf wetness and the maintenance of a 100% RH environment around sporangia for a sufficient length of time to establish infection in the leaf material. Previous work (Hartill et al., 1990) showed that post inoculation with *P. infestans*, if leaf wetness was interrupted during the first three hours, there was a significant negative impact on the resulting lesion numbers that was not seen in interruptions after the three-hour time point. This indicates that maintenance of a 100% RH environment for a specific time post inoculation is required to establish infection. This relates to the size of droplet used in an investigation, comparison of a 20µl and 5µl droplet showed that in low RH the larger droplet takes longer to evaporate and shows a greater IE. If the inoculum concentration is altered and the 20µl droplet has a concentration of 1000 spores ml and the 5µl droplet has a concentration of 5000 spores per ml, the larger droplet still showed the highest IE. The importance of selecting an appropriate droplet size and understanding the relationship between evaporation rate and maintenance of a 100%RH environment around the inoculum is thus important in these studies.

The genotypes of *P. infestans* in these investigations were representative of the population in GB. Eight isolates were used in preliminary investigations and four (2 x 6_A1 and 2 x 13_A2) were carried forward to the more extensive studies. The nature of the gradient plate and whole plant investigations was to establish the IE across a wide range of temperature, relative humidity and duration factors, this in turn meant that specific genotype performance was not a focus. The initial screening of the eight isolates was to establish the fitness of all eight and identify if there were any obvious or consistent differences in response between the genotypes. No consistent differences between genotypes were observed. Previous work on temperature and high humidity duration with larger subsets of each genotype also showed no consistent effect of genotype (Chapman, 2012) so these findings were not unexpected.

Decision support systems for late blight often use a 90% RH base threshold for indicating infection risk (Smith, 1956a, Bourke, 1955, Ullrich & Schrödter, 1966, Fry et al., 1983). Investigations into the IE below the 90% RH threshold has not been documented for modern genotypes of *P. infestans*, possibly due to the difficulty of controlling RH levels (Harrison, 1992). It was important to establish with experimental evidence that this criterion was suitable for the genotypes of *P. infestans* in the field. The gradient plate experiment assessed whether significant infection occurred below the threshold. The results showed that for RH levels below 90%, the IE was severely constrained. Thus, while the ability of *P. infestans* to infect at less than 90% RH was demonstrated, the limited advantages this offers under field conditions suggests that expansion of this criterion in a decision support system for potato late blight would not be warranted.

The gradient plate experiment was not the best model to investigate the factor of duration of exposure to relative humidity. The use of detached leaflets meant that all chambers were maintained at a 100% RH environment post exposure to maintain leaflet integrity over the seven-day period that the lesion developed. This was not representative of field conditions. The exposures to 90 and 100% RH for duration of 6, 11 and 24 hours were followed by placement into a 100% RH environment, logically negating the exposure factor. The previous investigation into droplet evaporation showed that at <85%RH droplets evaporated completely by a 6-hour time point, thus the effect of the 70 and 80% exposures for 6, 11 and 24 hours was confounded by droplet evaporation. Furthermore, while duration as a factor showed some significance in statistical analysis, examination showed the variation in infection efficiency was not consistently smaller or large for the different durations examined. This experimental model was thus not deemed the best for the investigation of duration as a factor on IE.

The criteria that influence the infection of *P. infestans* form a complex gradient making it challenging to determine the line when there is infection and when there is no infection. The assessment of which temperatures and RH criteria thus constitute high risk conditions may be considered subjective. The temperature threshold of the Smith Criteria, while shared with many DSSs (Bourke 1955, Bugiani, Cavanni & Ponti, 1993) was also recently implicated as the criterion of the Smith Period that required adjustment in the light of experimental evidence of infection below the 10°C threshold with contemporary *P. infestans* isolates (Cooke et al. 2012, Chapman, 2012). This was supported anecdotally from grower's observations. Syngenta's BlightCast tool (www.syngenta.co.uk/blightcast) was adjusted to a risk criterion which required two days with at least 11 hours of RH ≥ 90% and a minimum temperature of °8C in 2015 and 2016. Whether the ability to infect at lower temperatures is specifically related to new genotypes of *P. infestans* (See Hartill et al., 1990) or whether our ability to assess the impact of such infection criteria in the wider context of blight development in the field is open to debate. The gradient plate allowed for investigations of temperatures from 6 - 15°C and these temperatures were sustained throughout the experiment. While infection and lesion development were detected at lower temperatures, the infection efficiency and size of lesions was greatly reduced in comparison with higher temperatures. It was indeed only at temperatures above the 10°C threshold of the Smith Period where there was notable infection. Thus, though there was infection below the threshold, the rate was negligible and would not be considered a high-risk condition. While other experimental work, grower's anecdotes and Syngenta's BliteCast suggest the temperature threshold of the Smith Criteria as the criterion that needs adjustment, these investigations are more circumspect. The low IE and lesion growth may restrict infection and spread to very low levels under field conditions.

The whole plant experiment provided a model for investigating the effect of duration of RH exposure on infection. Whole plants exposed in chambers to 80, 90 or 100%RH could be removed and incubated in a glasshouse with a low RH comparable to field conditions during the day. As discussed above, the identification of risk conditions are subjective as infection is a gradient. The gradient of infection when exposed for 0 – 24 hours to high RH levels (90 and 100%) was not steep, indicating that there was a gradual change in IE relative to exposure time and thus IE below the 11-hour threshold of the Smith Period showed broadly similar levels of infection, i.e., the difference between IE of exposures for 11 and 6-hour durations was ~11% at 100%RH. This suggests that the Smith Period duration threshold may be the criteria, which if reduced, would lead to improvements in identification of high risk conditions for late blight development. The temperature factor of the whole plant experiments was affected by the experimental design requiring frequent entering and exiting of the growth chamber and thus not a focus of the final analysis. Genotype did not prove to be a highly significant factor either, as discussed previously, practical considerations resulted in few representative isolates of two lineages being examined in detail. Pathogen genotype was thus not a major point of investigation in these studies, but it indicates criteria for the two main *P. infestans* lineages in GB population currently.

3.6 CONCLUSIONS

These controlled environment experiment have examined the temperature, relative humidity and duration criteria required for contemporary GB genotypes of *P. infestans* to infect the commonly grown and moderately susceptible Maris Piper cultivar of potato. Specifically, the Smith Period DSS criteria have been investigated; a minimum temperature of 10°C, a relative humidity ≥90% and a duration of 11 hours. Glycerol-water solutions were utilised as a manner to easily control relative humidity levels in three differently sized chambers which were then kept in temperature-controlled environments. Detached leaflet experiments identified that the 90% RH level was suitable for identifying risk as IEs below this level were negligible. They also identified that the 10°C minimum temperature threshold was a suitable indicator of risk as at temperatures below this level the rate of infection was significantly slowed, and the lesion size reduced. Whole plant experiments were the best model to investigate duration of relative humidity as whole plants could be exposed to durations of high RH and then removed. These investigations identified that there was a gradient of IE based on duration of exposure to high RH and that the difference between IE at exposures of 11-hour durations and 6-hour durations to high RH was ~11%, indicating that high levels of risk occurred at shorter durations of exposure than the Smith Period identified.

3.7 Supplementary Tables

Supplementary Table 3.5: Gradient plate experiment temperature means, Std. Dev. And 95% CI for the gradient temperatures achieved in each column (temperature)

Column	Temperature Mean	Std Dev	95% CI
1	6.158	1.505	0.023
2	8.486	1.343	0.020
3	10.337	1.178	0.018
4	12.102	0.998	0.015
5	13.817	0.950	0.014
6	15.281	0.729	0.011

Supplementary Table 3.6: Gradient plate experiment relative humidity means, St. Dev. and 95% CI for the relative humidities of 70, 80, 90 and 100 at each different column (level of temperature)

Column	RH Intended	RH Mean	Std Dev	95% CI
1	70	74.018	6.258	0.626
1	80	81.075	3.998	0.400
1	90	85.578	4.705	0.471
1	100	103.557	6.504	0.555
2	70	78.392	6.112	0.647
2	80	82.812	6.421	0.687
2	90	92.88	3.255	0.348
2	100	99.744	2.739	0.207
3	70	79.554	15.275	1.528
3	80	83.232	5.206	0.521
3	90	91.118	5.299	0.567
3	100	100.2	4.059	0.346
4	70	78.059	7.726	1.093
4	80	90.025	12.285	1.419
4	90	94.537	3.837	0.362
4	100	99.490	2.333	0.176
5	70	83.688	14.161	1.792
5	80	81.769	1.744	0.221
5	90	93.626	4.817	0.482
5	100	99.496	1.796	0.123
6	70	73.856	8.642	0.924
6	80	87.311	5.908	0.632
6	90	92.260	10.068	
6	100	99.635	2.232	0.175

Supplementary Table 3.7: Gradient Plate experiment results from regression model prediction for lesion size

Column	RH	13_A2	13_A2 (2)	6_A1	6_A1 (2)
1	70	-0.0007	0.0001	-0.0007	0.0001
	80	0.0001	0	-0.0013	0
	90	0.0073	0.0081	-0.0005	0.0008
	100	-0.0088	0.0035	-0.009	0.0041
2	70	0.0004	0.0011	-0.0027	0.0018
	80	-0.0009	0.0035	0.003	0.0005
	90	0.0045	0.0053	0.0018	0.0025
	100	0.0071	0.0004	0.0158	-0.002
3	70	0.0117	0.0004	-0.0016	0.0004
	80	0.0161	0.0033	0.008	0.0087
	90	0.0355	0.0141	0.017	0.0062
	100	0.0354	0.0268	0.0207	0.0742
4	70	0.0023	0.0036	0.0011	0.0305
	80	0.0008	0.0032	0.0062	0.1333
	90	0.063	0.0229	0.0292	0.039
	100	0.1726	0.128	0.2746	0.282
5	70	0.014	0.0034	0.0075	0.0425
	80	0.0004	0.0341	0.0337	0.1253
	90	0.0149	0.129	0.0802	0.0361
	100	0.8175	0.8033	0.7443	1.1799
6	70	0.0054	0.0198	0.0901	0.0025
	80	0	0.0054	0.0082	0.1359
	90	0.1489	0.0491	0.1428	0.3517
	100	0.8673	1.3387	1.8666	2.0083

Minimum standard error of difference	0.06793
Average standard error of difference	0.08778
Maximum standard error of difference	0.11657

4 CHAPTER FOUR: TESTING ALTERNATIVE RISK CRITERIA TO IDENTIFY HIGH RISK CONDITIONS FOR POTATO LATE BLIGHT DEVELOPMENT IN GREAT BRITAIN

4.1 ABSTRACT

The Smith Period has been used as the national warning system for potato late blight in Great Britain for over 60 years. It is defined as two consecutive days each with a minimum temperature ≥10°C and at least 11 hours of relative humidity ≥90%. The performance of the Smith Period as a tool for forecasting late blight outbreaks was recently examined using a back-testing framework- with historical national-scale outbreak and weather data (Chapter 2). It was ranked as a 'fair' diagnostic tool and showed significant variation in performance across the country. The core temperature and humidity criteria of the Smith Period were refined using a series of controlled environment experiments, which revealed that blight lesions can develop after shorter durations to high relative humidity than those prescribed by this warning system (Chapter 3). In this study we evaluate five candidate replacement models for the Smith Period, comprised of alternative temperature and relative humidity thresholds suggested by the results of the experimental analyses. Model performance was assessed using a combination of frequency analysis, ROC analysis and mapping. The best prediction outcome was obtained by lowering the duration of relative humidity to 6 hours on each of the two consecutive days, yielding an area under the ROC curve of 0.973 (95% CI = 0.943–1.000), an alert frequency of approximately 1 in 7 days, and a marked improvement in uniformity of performance across the country. This model has been named the 'Hutton Criteria' and it now forms the new national warning system for late blight in Great Britain, with predictions provided free of charge via the Agricultural and Horticulture Development Board Potatoes 'Blightwatch Service.'

4.2 INTRODUCTION

Late blight is one of the most devastating diseases of potato; in ideal conditions it can spread rapidly destroying an entire crop in a week and cause great financial loss to the grower (Hijmans, Forbes & Walker, 2000, Guenthner, Michael & Notle, 2001, Haverkort et al., 2008). Growers around the world generally employ a prophylactic approach to disease management, with regular fungicide applications throughout the year (Nielson, 2004). In Great Britain (GB) as in many countries, there are regulations regarding fungicide use; i.e. some products may only be used a certain number of times per year or for a limited period. There is also market and public pressure to reduce heavy reliance on fungicides as we become a more environmentally conscientious society. Decision support systems (DSS) are tools developed for agriculture to provide information on disease risk to aid in crop management. They are typically developed experimentally and rigorously tested so that the grower can confidently rely on their advice. DSSs for potato late bight (PLB) identify high risk environmental conditions for disease development and conversely those periods which are not high risk (Cooke et al., 2011, Arora, Sharma & Singh, 2014). Each country generally has their own DSS for potato late blight, comprised of core temperature and relative humidity criteria, and some have been extended to incorporate information on fungicide treatments, varietal resistance, solar radiation and in field sporangia detection (Chapter 1, Cao, Ruckstuhl & Forrer, 1997, Forbes, 2004, Hu, Zhu & Cao, 2012, Aurora, Sharma & Singh, 2014). The core temperature and relative humidity criteria vary slightly, as they are tailored to the local *Phytophthora infestans* population and weather conditions, the nature of the data available to issue alerts, and the level of interaction and knowledge of growers in each country.

The Smith Period, developed in the 1950’s, was the most widely known and used DSS in GB, until 2016. A Smith Period is defined as two consecutive days where for each day the minimum temperature is ≥10°C and there are at least 11 hours of RH ≥ 90% (Smith, 1956). The Agricultural and Horticultural Development Board Potatoes (AHDB Potatoes) fund a national ‘Blight Watch’ service in GB that provides free notifications to growers when a Smith Period alert has occurred in their specific postcode district. The Smith Period was recently evaluated for the first time since its inception using a historical twelve-year data set of recorded PLB outbreaks across GB and corresponding UK Meteorological Office (UKMO) data. The Smith Period was ranked as a ‘fair’ diagnostic tool for indicating high risk periods for late blight development and showed significant variation in performance across the different climatic districts of GB (Chapter 2).

The temperature, relative humidity level and duration criteria required to define high risk conditions for potato late blight were recently re-evaluated using isolates of *P. infestans* representative of the contemporary GB (Chapter 3). The results showed negligible levels of infection below the 10°C minimum temperature threshold of the Smith Period and below the 90% RH threshold, but significant infection at durations of high relative humidity below the 11-hour threshold. This result agreed with the back-testing analysis (Chapter 2) of the Smith Period, which consistently showed mean temperatures above 10°C and durations of high relative humidity below 11 hours in the weeks leading up to an outbreak. These two sets of analyses suggest that the Smith Period could be improved by shortening the duration of high humidity required to trigger a risk warning.

Our goal here is to: (i) develop alternative models for forecasting the risk of late blight development, and (ii) assess the performance of the models by repeating the back-testing analysis with historical late bight outbreak and weather data previously used to assess the Smith Period (Chapter 2). The alternative models are developed from prior experimental work (Smith, 1956(i), Crosier, 1934, Chapman 2012) and the results of our own controlled environment experiments (Chapter 3). Model performance was compared to the Smith Period over a period of 12 years (2003-2014) in each of the different climatic districts of Great Britain through a combination of alert frequency analysis, receiver operator characteristic (ROC) curve analysis and GIS mapping techniques0.

4.3 MATERIALS AND METHODS

4.3.1 Data Sets

4.3.2 Historical late blight outbreak data

Fight Against Blight (FAB) an AHDB Potatoes funded program has recorded PLB outbreaks across GB since 2003. Blight scouts sent samples of infected leaves and details of PLB outbreaks from across GB to the James Hutton Institute, where each is recorded, and the sample genotyped. There were >2000 documented outbreaks between 2003 – 2014 which will be used for a back-testing analysis of candidate models in this study. Disease pressure varied from year to year and this is reflected in the number of reported outbreaks each year: 104, 143, 99, 162, 281, 204, 143, 82, 179, 344, 66, and 258 for the years 2003–2014 respectively. Summary statistics of the FAB data set from 2003 – 2014 can be found in Chapter 2.

4.3.3 Historical weather data

The UKMO calculated and provided the Smith Period alerts for the national Blightwatch warning system between 2003 - 2014. They provided a historical weather data set for this period from the 1st of April – 30th of September (the growing season) each year. These data were used in the evaluation of the Smith Period (Chapter 2) and are used here to compare alternative models. The data are comprised of historical observations of daily minimum temperature and number of hours per day of relative humidity ≥ 90% for 652 different locations across Great Britain, recorded from sensors ~1.25 meters above ground height. Each of the 652 locations may be an interpolation of data from several Met office sites. The >3000 postcode districts of Great Britain were each assigned to one of these representative 652 data points based on location.

4.3.4 Methods

The historical data sets were used to examine the performance of alternative models to the Smith Period using a combination of MATLAB, ArcGIS and GenStat 18th edition.

4.3.5 UKMO Climatic Districts

The UKMO has nine defined climatic districts of Great Britain: (1) Scotland North (2) Scotland West (3) Scotland East (4) North West England and North Wales (5) North East England (6) Midlands (7) South West England and South Wales (8) South East England and (9) East Anglia, (Figure 1). These districts have definably different (between) or similar (within) climatologies and were used to create sub groups of the PLB outbreak data for evaluation. Data from the UKMO for each year in these climatic districts summarizing temperature, sunshine, rainfall and frost was assessed in Chapter 2.

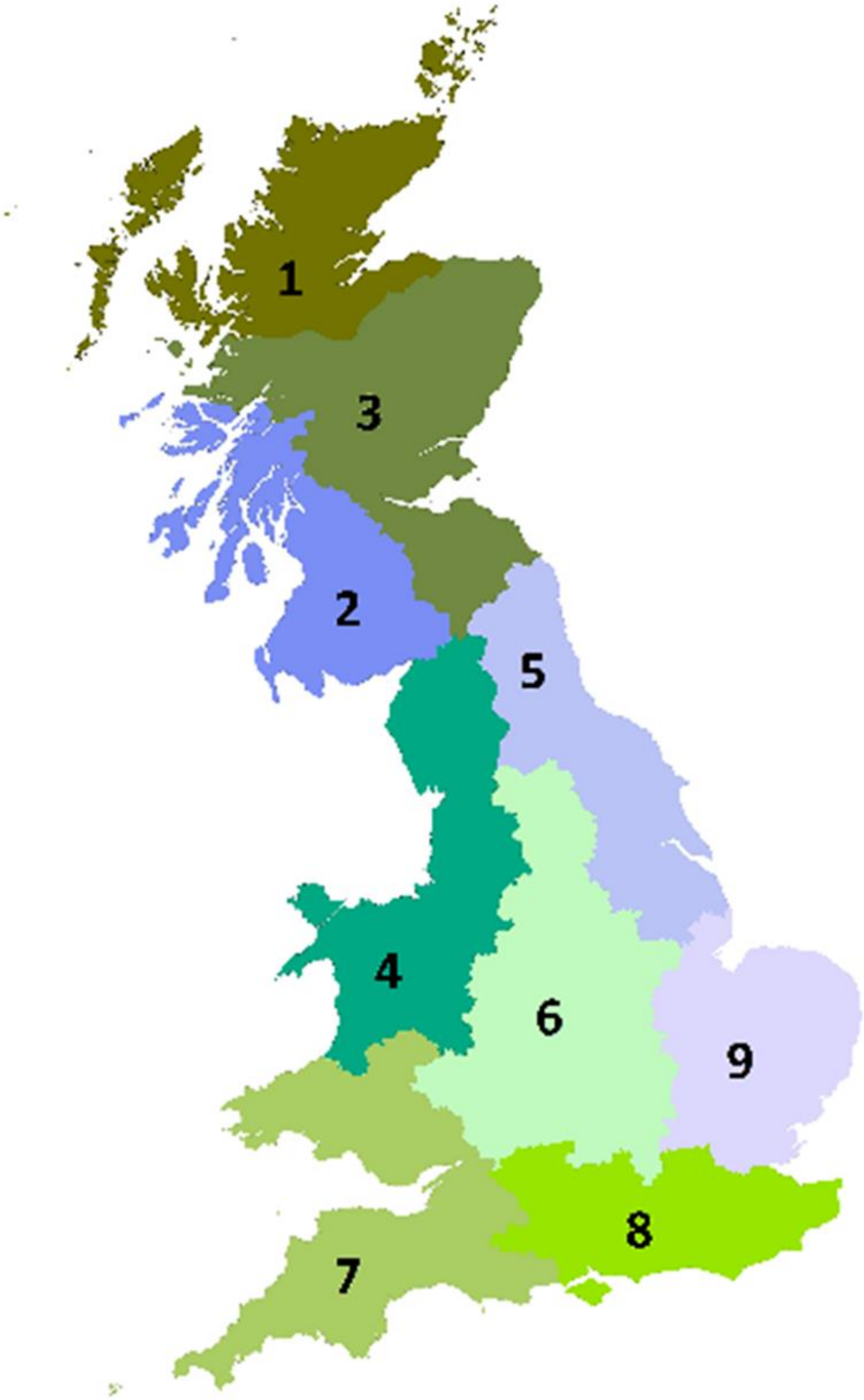

Figure 2.1: Climatic districts of Great Britain defined by the United Kingdom Met Office. (1) Scotland north, (2) Scotland west, (3) Scotland east, (4) England northwest and northern Wales, (5) northeast England, (6) Midlands, (7) southeast England and southern Wales, (8) southeast England, (9) east Anglia

4.3.6 Alternative Criteria

Five models of risk criteria were developed based on the historic performance of the Smith Period (Chapter 2), results of controlled environment experiments to refine the infection parameters of *P. infestans* with current genotypes (Chapter 3), and personal communication from growers and industry feedback, (Table 4.1). All models consist of two consecutive days where specific temperature and relative humidity criteria need to be met in full. Models 1 and 3 were 'low temperature models' compared to the Smith Period. Although our previous analyses provided little evidence to suggest that lower temperature models would be more effective, they are included here as it was believed in research and industry that current genotypes of *P. infestans* may be more aggressive at lower temperatures, thus potentially explaining why the Smith Period was not as effective as desired. Syngenta have in recent years released a new lower temperature model, which is in fact the same as Model 1. Model 2 was a shorter duration of relative humidity model, where the 10°C minimum temperature threshold was maintained, and the relative humidity duration shortened from 11 hours to 6 hours; this was selected based on historic research into high relative humidity durations (Chapter 1), the trends in mean relative humidity durations in the days prior to outbreaks in the FAB historic outbreak data set (Chapter 2), and the controlled environment experiments we conducted that showed high levels of infection below the 11 hour threshold set by the Smith Period (Chapter3). Models 4 and 5 had both the temperature and relative humidity duration levels lowered to, 8°C and 6 hours RH and 6°C and 6 hours RH, respectively (Table 4.1).

Table 4.1: Alternative models to be examined historically for performance as indicators of high risk periods for potato late blight development

Model	Minimum Temperature (°C):	Relative Humidity (≥90%) Duration (Hrs):
Smith Period	10	11
1	8	11
2	10	6
3	6	11
4	8	6
5	6	6

*Each model consists of two consecutive days of both the temperature and relative humidity criteria

4.3.7 Frequency of Alerts

Occurrence of alerts is an important consideration for a decision support tool; if the risk alerts are too frequent it is of little value to a grower. The new models are expected to be more sensitive than the Smith Period as the environmental envelope defined by the temperature and humidity criteria has been widened in each. The percentage of all growing days (April 1 – September 30) receiving an alert during the entire study period (2003-2014) at locations that reported outbreaks was calculated for each model and results grouped according to climatic district. The percentage of days receiving an alert prior to the date of observation was calculated at each outbreak location for the entire study period, and results grouped according to climatic district. This removed data from areas outside of potato growing regions and removed data later in season where there may be a higher frequency of alerts, but the crop is established and protected by a regular fungicide spray regime. The mean number of alerts in the period prior to reported outbreaks were calculated and results grouped by year and climatic region.

4.3.8 Alert Frequency and Outbreak Maps

Inverse distance weighted (IDW) interpolation mapping in ArcGIS was used to create heat maps of Great Britain for the total number of alerts produced by each model during this study period. These surface maps predict the weight of pixels in-between known data points, where the nearest neighbour data point has the largest impact on prediction and this diminishes the further the known data point is from the point being predicted (Johnston, Ver Hoef, Krivoruchko & Luca, 2001, Childs, 2004, Blanco, de Serres, Cárcaba, Lara & Fernández-Bustillo, 2012). They are constructed from daily data from the 652 UKMO locations across Great Britain and thus produce smooth surface plots. IDW maps for the outbreak data were also constructed, showing outbreaks receiving alerts and outbreaks not receiving alerts. These maps were coarser due to irregular distribution of outbreaks across GB.

4.3.9 Receiver Operator Characteristic Curve Analysis

Receiver operator characteristic (ROC) curve analysis was used to quantify the performance of the Smith Period as a diagnostic tool for indicating high risk periods for potato late blight. This method of analysis is described in Chapter 2.3.2.5. The same analysis is repeated here to compare the performance of the new models for forecasting outbreaks against the Smith Period, using historical FAB outbreak data set (>2000 outbreaks, from 2003 – 2014) and corresponding UKMO weather data set. Results are grouped according to year and climatic district of GB.

4.4 RESULTS

4.4.1 Alert Frequency

The southwest of England & south Wales region had the highest percentage of days receiving alerts for all models tested while western Scotland had the lowest percentage of days receiving alerts (Figure 4.2). The percentage of days across GB between 2003 – 2014 receiving Smith Period, model 1, 2, 3, 4 and 5 alerts was 15, 19, 27, 22, 37 and 44% respectively. The percentage of days prior to outbreaks (1st April to date of outbreak) across GB between 2003 – 2014 receiving Smith Period, model 1, 2, 3, 4 and 5 alerts was 7, 10, 16, 12, 24 and 30% (Figure 4.3). The southwest of England and south Wales again received the highest percentage of alerts and Scotland north received the lowest.

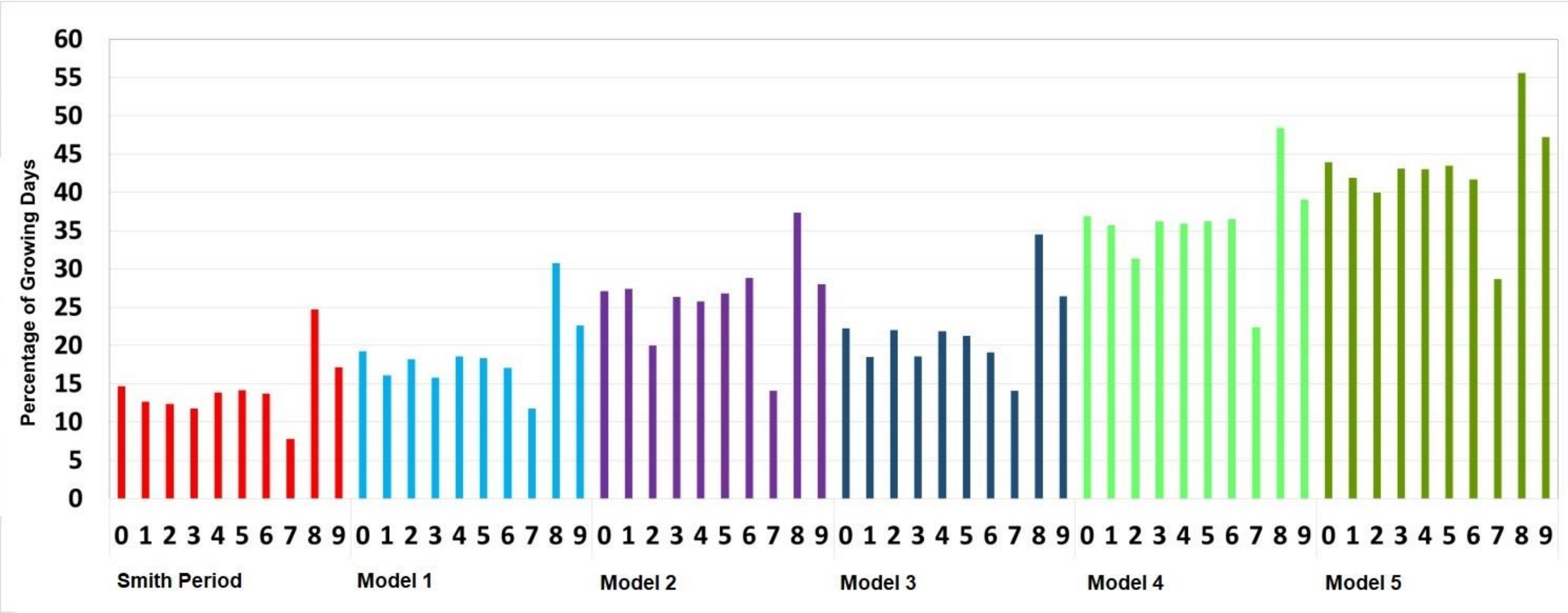

Figure 4.2: Percentage of all growing days (1st April - 30th September, 2003 – 2014) at sites of potato outbreaks that received a Smith Period for Model 1 – 5 alert for the climatic districts of Great Britain: (0) GB, (1) east Anglia, (2) eastern Scotland, (3) midlands, (4) northeast England, (5) northwest England and northern Wales, (6) southeast England, (7) Scotland north, (8) southwest England and south Wales and (9) western Scotland

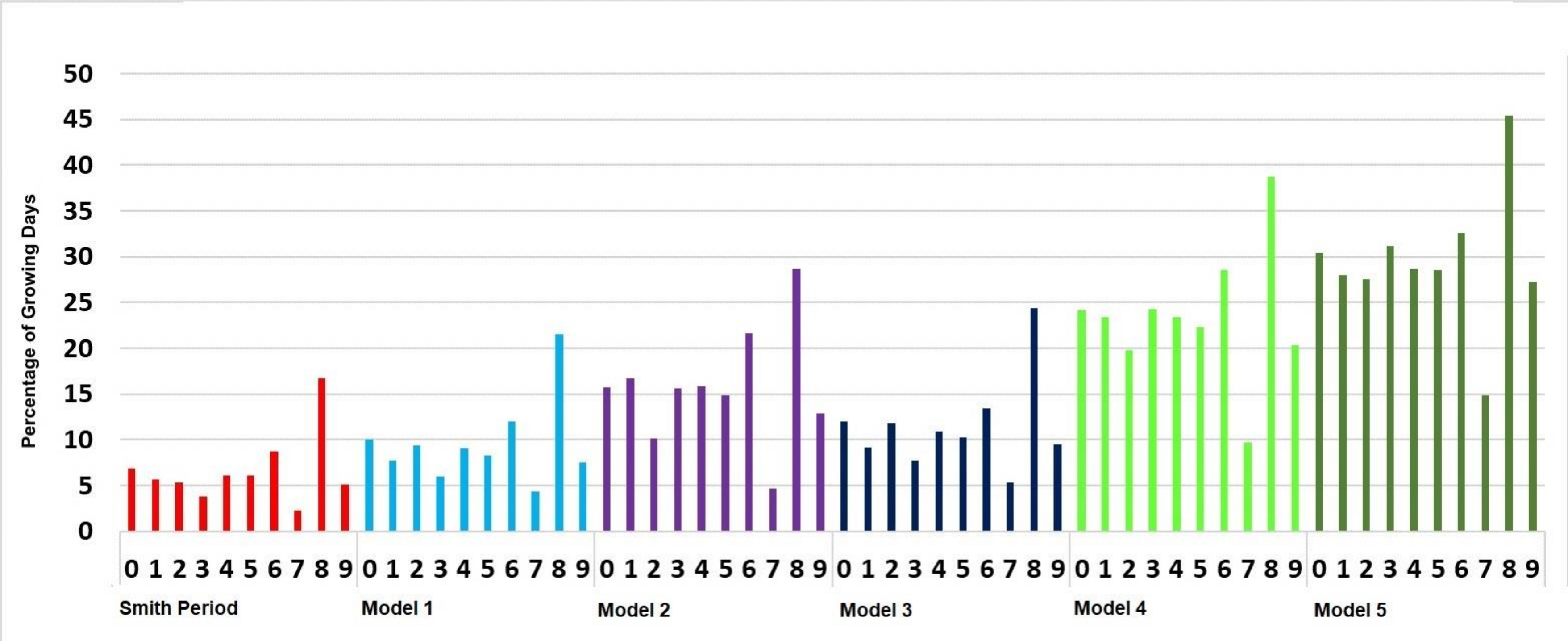

Figure 4.3: Percentage of days prior to reported potato late bight outbreaks (1st April to date of outbreak) that received either Smith Period for Model 1-5 alerts, grouped according to: (0) GB, (1) east Anglia, (2) eastern Scotland, (3) Midlands, (4) northeast England, (5) northwest England and northern wales, (6) south east England, (7) Scotland north, (8) southwest England an southern Wales and (9) western Scotland

Significant temporal and spatial variation are apparent in the mean number of alerts in the 28 days prior to an outbreak for all models when results are grouped according to year and climatic region (Table 4.2 A-F). The Smith Period, Model 1 and Model 3 generate low numbers of alerts in the 28 days prior to reported outbreaks while models 4 and 5 generate a greater number of alerts. Model 2 produced a high number of alerts in some years (2007, 2008, 2012) but not others (2005, 2013), which reflects the blight pressure in these ears, as is evident in FAB PLB outbreak numbers.

Table 4.2.A: Mean number of Smith Period alerts in a 28-day window prior to outbreaks for each climatic region and year, * = no data.

Smith Period:									
Region	EA	ES	Mid	NEE	NWENW	SEE	SN	SWESW	WS
2003	0.85	1.95	1.6	2.17	4.33	1.33	*	3.22	0
2004	2.62	5.65	1.7	4.94	4.41	2.86	0.5	8.11	*
2005	1.38	1.35	0.5	0.78	1.87	2	*	4.88	2
2006	1.18	2.46	1.2	3.14	1.21	1.44	*	4.58	*
2007	6.56	5.77	2.6	3.7	1.57	7.58	*	5.45	2.67
2008	3.78	5.83	1.96	1.27	2.56	4	*	5.16	4.5
2009	2	3.18	1.6	1.4	1.78	4.86	*	9.23	0.68
2010	1.8	0.82	1.2	*	6.92	2.25	1.5	9.5	0.33
2011	0	2.7	3.67	0	3.57	*	1.5	7	*
2012	4.19	6.24	5.33	6.1	4.55	4.33	1	8.11	6.2
2013	1.5	4.67	1.5	1.5	0.14	2	*	5.36	0.75
2014	1.35	1.72	0.96	0.9	0.79	2.33	*	2.09	1

Table 4.2.B: Mean number of Model 1 alerts in a 28-day window prior to outbreaks for each climatic region and year, * = no data.

Model 1:									
Region	EA	ES	Mid	NEE	NWENW	SEE	SN	SWESW	WS
2003	0.91	2.25	2.4	4.22	6	2.67	*	5.11	0
2004	3	6	2.3	5	4.53	3.43	1	9	*
2005	1.48	1.94	0.5	0.78	2.13	2.17	*	5.88	2.75
2006	1.75	3.91	1.2	2.57	1.79	3.22	*	6.42	*
2007	7.02	10.04	3.03	5.44	2.03	9.42	*	7	4
2008	5.35	7.14	2.71	1.6	3.06	5.4	*	6.23	5.25
2009	2.11	4.11	2.3	1.6	2.44	5.71	*	10.7	0.67
2010	2.3	2.23	3.2	*	7.67	2.25	2.5	10.79	0.33
2011	0	3.86	3.83	0.5	4.57	*	3	8.77	*
2012	4.55	8.89	6.36	6.8	5.29	5.07	3	12.09	9
2013	1.5	5	1.7	1.5	0.29	2.2	*	6	1
2014	2.23	2.09	2.83	2.6	1.5	2.56	*	4.59	2.5

Table 4.2.C: Mean number of Model 2 alerts in a 28-day window prior to outbreaks for each climatic region and year, * = no data.

Model 2:									
Region	EA	ES	Mid	NEE	NWENW	SEE	SN	SWESW	WS
2003	3.59	6.25	4.6	5.17	8.67	3.33	*	5.89	2
2004	10.95	7.82	6.78	12.78	9.53	8.43	0.5	13.44	*
2005	3.86	4	5	3.33	4.33	4.67	*	10.63	4.25
2006	4	4.82	3.5	7.29	2.36	3.17	*	8.33	*
2007	11.49	7.75	11.43	12.09	7	12.97	*	10.31	6.5
2008	6.96	11.23	8.5	6	8.13	6.6	*	8.77	12.25
2009	9.42	8.34	11.33	5.2	5.78	13.14	*	14.23	4
2010	3.9	2.64	4	*	13.67	8	3	17.07	4.67
2011	4.83	5.04	4.17	1	7.14	*	2	11.46	*
2012	8.89	8.32	9.82	8.69	8.58	10.96	4	10.49	12
2013	6.25	7.33	4.8	6.5	5.64	8	*	11.64	5.25
2014	4.81	5.54	5	3.7	3.44	5.78	*	5.14	3.67

Table 4.2.D: Mean number of Model 3 alerts in a 28-day window prior to outbreaks for each climatic region and year, * = no data.

Model 3:									
Region	EA	ES	Mid	NEE	NWENW	SEE	SN	SWESW	WS
2003	0.97	2.25	2.4	4.67	6.83	2.67	*	5.33	0
2004	3.15	6.24	2.3	5	4.53	3.57	1.5	9.11	*
2005	1.48	2.35	1	0.78	2.13	2.17	*	6.19	3
2006	1.79	4.09	1.2	2.71	2.93	3.48	*	6.83	*
2007	7.62	10.73	3.6	5.87	2.13	9.58	*	7.31	4
2008	5.44	7.79	2.88	1.6	3.19	5.4	*	6.65	5.5
2009	2.11	4.29	2.48	1.8	2.44	5.71	*	11.15	1.67
2010	2.3	3.23	3.4	*	7.67	2.25	3	10.79	0.67
2011	0	4.02	4.17	2	5.71	*	3	8.85	*
2012	4.6	10.1	6.85	6.89	5.71	5.63	4	12.91	9
2013	1.5	5	1.7	1.5	0.29	2.4	*	6	1
2014	2.77	2.28	3.5	3.2	1.82	2.89	*	5.23	3.67

Table 4.2.E: Mean number of Model 4 alerts in a 28-day window prior to outbreaks for each climatic region and year, * = no data.

Model 4:									
Region	EA	ES	Mid	NEE	NWENW	SEE	SN	SWESW	WS
2003	4.82	8.3	6.8	9.33	13.5	5.33	*	10.11	2
2004	12.15	9.12	8.48	14.67	11.06	9.14	1.5	15.11	*
2005	4.59	6.06	6.5	4.89	6.2	5.17	*	12.81	6.25
2006	7.38	8	5.1	8.57	4.29	7.22	*	11.17	*
2007	14.48	13.69	13.17	15	9.33	15.16	*	13.62	11.33
2008	10.39	15.76	10.96	8.67	10.63	8.6	*	12.07	14
2009	10	12.46	16.33	7.4	8	15	*	16.62	4.33
2010	5	6.09	8.2	*	16.33	8.25	6	19.93	5.67
2011	4.83	9.88	9.17	4	11.43	*	3.5	16.23	*
2012	11.81	13.53	13.98	11.07	11.11	13.7	12	16.49	16
2013	8.25	9.67	6.4	8	6.21	9.2	*	14	6.5
2014	7.42	7.98	9.5	8	7.71	7.67	*	9.5	6.67

Table 4.2.F: Mean number of Model 5 alerts in a 28-day window prior to outbreaks for each climatic region and year, * = no data.

Model 5:									
Region	EA	ES	Mid	NEE	NWENW	SEE	SN	SWESW	WS
2003	5.47	8.85	9.4	10.72	15.33	5.33	*	11.11	2
2004	13.28	10.06	9.7	15	11.82	9.43	3.5	15.8	*
2005	5	7.24	7.5	5	7.2	5.5	*	13.75	8
2006	8.71	9.46	5.8	9.57	6.79	8.57	*	12.67	*
2007	16.59	15.47	14.33	16	9.9	15.52	*	14.52	14.5
2008	11.26	16.99	11.46	8.93	12.19	9.2	*	13.45	14.5
2009	10.16	13.98	18	7.8	9	15.86	*	18.23	5.33
2010	5.2	8.68	9.8	*	17	8.25	9.5	20	6.67
2011	5	14.13	10.67	7.5	14.57	*	6.5	18	*
2012	12.66	16.47	15.51	12.62	12.82	15.22	14	19.37	17.6
2013	8.5	10	7	8	6.43	9.4	*	14.27	7.25
2014	8.46	10.13	11.92	9.4	9.5	8.79	*	12.5	9

4.4.2 Alert Frequency Maps

IDW interpolation maps of the number of Smith Period and model 1 – 5 alerts across GB are shown in Figure 4.4. The Smith Period map shows that many central regions received a low number of alerts while coastal regions received a greater number of alerts. Models 4 and 5 produce a high number of alerts across the entire country except for the Cairngorm mountains in Scotland. The two low temperature models, 1 and 3, show very similar patterns of alerts to the Smith Period. Note that the Smith Period showed highly significant variation in performance across the climatic districts of GB in Chapter 2. Model 2 shows the most uniform distribution of alerts across GB, without the high intensity of alerts seen with models 4 and 5.

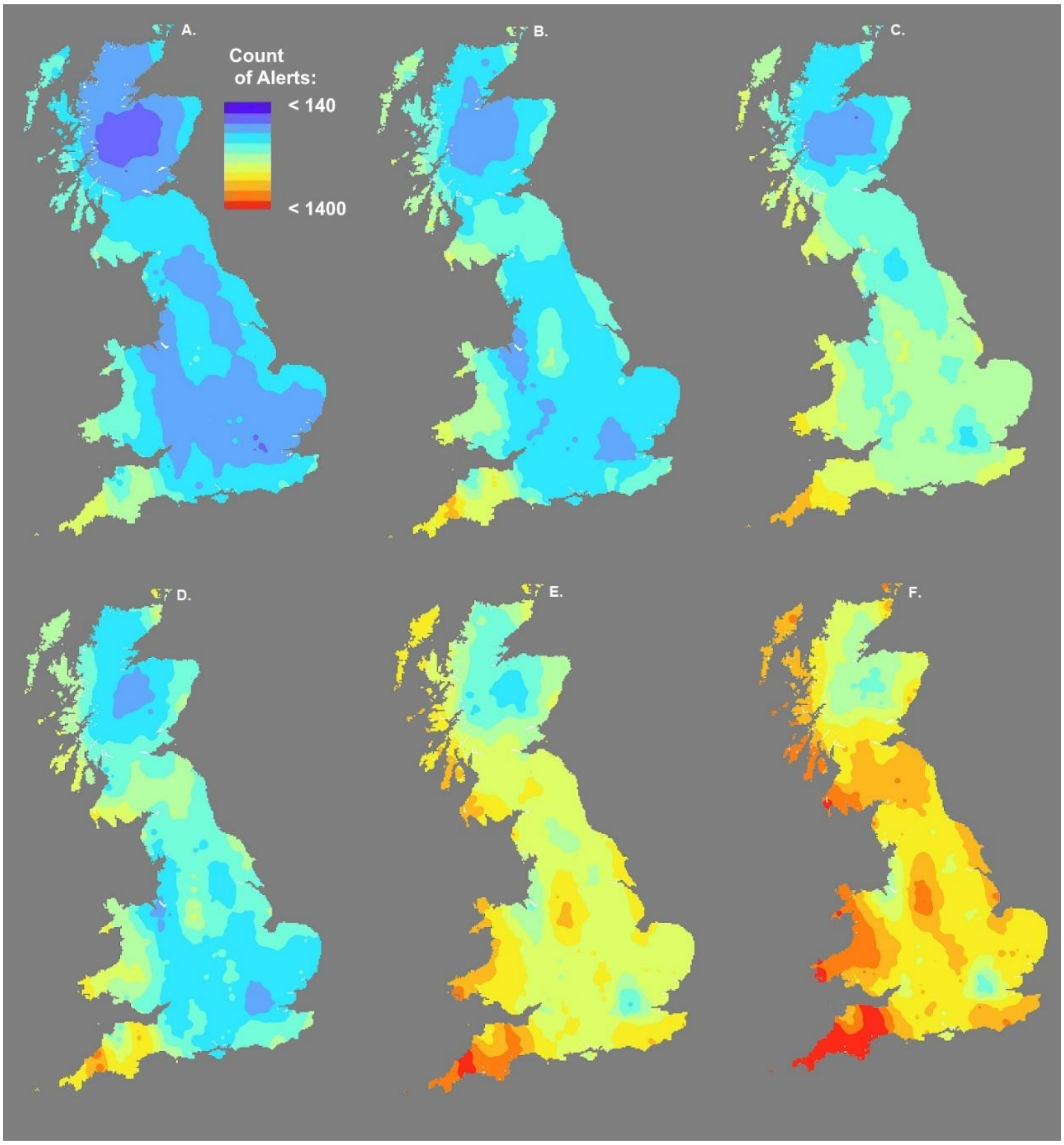

Figure 4.4: Inverse distance weighted (IDW) maps showing the total number of (A) Smith Periods, (B) Model 1, (C) Model 2, (D) Model 3, (E) Model 4 and (F) Model 5 alerts calculated using 652 UKMO data points spanning April 1l – September 30, 2003 – 2014.

4.4.3 Receiver Operator Characteristic Curve Analysis

ROC curves for the entire outbreak data set (>2000 outbreaks, 2003-2014) reveal an improved performance of models 1-5 over the Smith Period (Figure 4.5). This is expected as models 1-5 have a reduced temperature and/or relative humidity thresholds in comparison to the Smith Period, i.e. they are widening the envelope of environmental conditions that define a risk period, and therefore successfully forecasting more outbreak events (Figure 4.5). The AUROC values are as follows: Smith Period [0.686 (95% CI = 0.540 - 0.8.32)], Model 1[0.823 (95 CI = 0.712 – 0.934)], Model 2[0.973 (95% CI =

0.943 – 1.000)], Model 3[0.849 (95% CI = 0.749 – 0.950)], Model 4[0.994 (95% CI = 0.983 – 1.000)], Model 5[0.999 (95% CI = 0.996 – 1.000)].

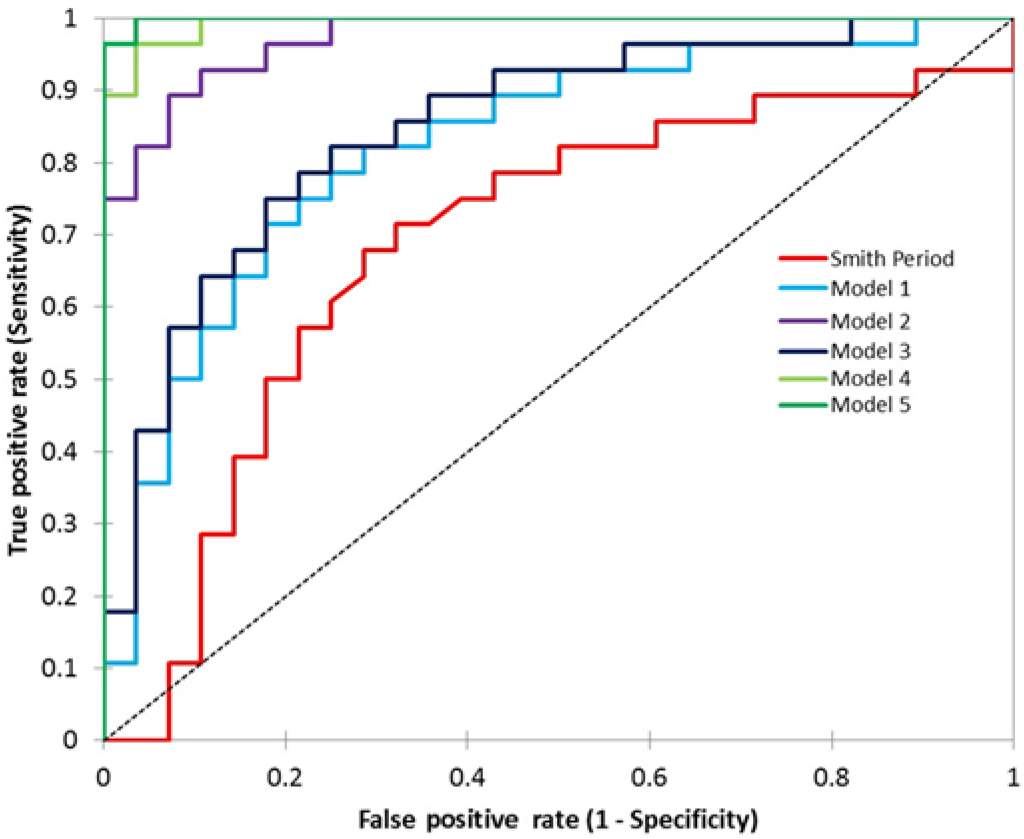

Figure 4.5: ROC curves for the Smith Period and models 1-5, to determine performance as diagnostic tools for indicating high risk of potato late bight, using FAB outbreak data from 2003 – 2014 for all climatic districts.

An ANOVA of AUROC results for individual years and climatic districts provided a more detailed model comparison (Table 4.3.A-F).

Table 4.3.A: AUROC values for the Smith Period for each year (2003 – 2014) and climatic region, * = no data.

Smith Period:									
Year/Region:	EA	ES	Mid	NEE	NWENW	SEE	SN	SWESW	WS
2003	0	0.661	0	0.861	0.999	0	*	0.751	0
2004	0.693	0	0	0.982	0.872	0.666	0.184	0.987	*
2005	0.36	0.397	0.052	0.128	0.306	0.385	*	0.87	0.006
2006	0	0.774	0.01	0.425	0	0.434	*	0.613	*
2007	0.952	0.886	0.816	0.663	0.409	0.861	*	0.957	0.708
2008	0.823	0.92	0.774	0.281	0.806	0.798	*	0.961	0.857
2009	0.355	0.642	0.582	0.704	0.416	0.714	*	0.955	0
2010	0.848	0.217	0.003	*	0.959	0.862	0.921	0.997	0
2011	0	0.602	0.742	0	0.759	*	0.207	0.974	*
2012	0.864	0.93	0.938	0.98	0.935	0.94	0.031	0.982	*
2013	0.108	0.827	0.56	0.077	0	0.485	*	0.681	0.688
2014	0.207	0.476	0	0	0	0.927	*	0.642	0

Table 4.3.B: AUROC values for Model 1 for each year (2003 – 2014) and climatic region, * = no data.

Model 1:									
Year/Region:	EA	ES	Mid	NEE	NWENW	SEE	SN	SWESW	WS
2003	0	0.668	0.617	0.919	0.999	0	*	0.778	0
2004	0.742	0.703	0.319	0.892	0.872	0.671	0.76	0.987	*
2005	0.434	0.481	0.052	0.128	0.306	0.628	*	0.874	0.167
2006	0.078	0.877	0.01	0.568	0.085	0.518	*	0.722	*
2007	0.952	0.962	0.855	0.86	0.513	0.888	*	0.981	0.959
2008	0.825	0.957	0.851	0.411	0.888	0.811	*	0.966	0.954
2009	0.379	0.874	0.713	0.88	0.816	0.714	*	0.989	0
2010	0.9	0.645	0.679	*	0.959	0.862	0.921	0.999	0
2011	0	0.854	0.742	0.108	0.862	*	0.73	0.979	*
2012	0.906	0.985	0.954	0.98	0.95	0.946	*	0.992	0.982
2013	0.108	0.827	0.656	0.077	0	0.485	*	0.759	0.688
2014	0.42	0.619	0.783	0.481	0.159	0.927	*	0.777	0.531

Table 4.3.C: AUROC values for Model 2 for each year (2003 – 2014) and climatic region, * = no data.

Model 2:									
Year/Region:	EA	ES	Mid	NEE	NWENW	SEE	SN	SWESW	WS
2003	0.643	0.945	0.449	0.983	1	0.214	*	0.962	0.207
2004	0.992	0	0.936	0.989	0.999	0.994	0.184	0.999	*
2005	0.886	0.821	0.569	0.511	0.773	0.927	*	1	0.064
2006	0.876	0.864	0.884	0.813	0.008	0.668	*	0.896	*
2007	1	0.964	0.999	0.995	0.976	0.969	*	1	0.89
2008	0.915	0.978	0.986	0.974	1	1	*	0.994	0.99
2009	0.974	0.949	0.999	0.926	0.903	1	*	1	0.92
2010	0.902	0.534	0.904	*	1	0.987	*	1	0.519
2011	0.898	0.957	0.778	0.255	0.906	*	0.867	0.999	*
2012	0.99	0.966	0.995	0.992	1	0.999	0.403	0.995	0.995
2013	0.905	1	0.948	0.851	0.896	0.994	*	0.97	0.934
2014	0.895	0.793	0.954	0.716	0.938	0.978	*	0.959	0.985

Table 4.3.D: AUROC values for Model 3 for each year (2003 – 2014) and climatic region, * = no data.

Model 3:									
Year/Region:	EA	ES	Mid	NEE	NWENW	SEE	SN	SWESW	WS
2003	0	0.668	0.617	0.919	0.999	0	*	0.778	0
2004	0.742	0.703	0.319	0.892	0.872	0.671	0.76	0.987	*
2005	0.434	0.667	0.087	0.128	0.306	0.628	*	0.948	0.167
2006	0.083	0.877	0.01	0.79	0.336	0.518	*	0.724	*
2007	0.959	0.969	0.868	0.871	0.513	0.888	*	0.981	0.959
2008	0.825	0.962	0.862	0.411	0.924	0.811	*	0.97	0.954
2009	0.379	0.884	0.713	0.88	0.816	0.714	*	0.989	0
2010	0.9	0.851	1	*	0.959	0.862	0.921	0.999	0.63
2011	0	0.887	0.765	0.143	1	*	0.73	0.99	*
2012	0.906	0.989	0.959	0.98	0.95	0.953	0.449	0.994	0.982
2013	0.108	0.827	0.656	0.077	0	0.485	*	0.759	0.688
2014	0.524	0.626	0.848	0.481	0.297	0.927	*	0.821	0.775

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Table 4.3.E: AUROC values for Model 4 for each year (2003 – 2014) and climatic region, * = no data.

Model 4:									
Year/Region:	EA	ES	Mid	NEE	NWENW	SEE	SN	SWESW	WS
2003	0.739	0.959	0.852	0.993	1	1	*	0.987	0.207
2004	0.995	0.865	0.994	0.999	0.999	0.995	0.79	0.999	*
2005	0.739	0.96	0.601	0.575	0.927	0.952	*	1	0.925
2006	0.984	0.956	0.919	0.888	0.894	0.879	*	0.946	*
2007	1	0.995	1	0.999	0.99	0.969	*	1	0.999
2008	0.918	0.999	0.996	0.999	1	1	*	1	0.99
2009	0.974	0.999	1	0.996	0.949	1	*	1	0.92
2010	0.957	0.923	1	*	1	0.987	0.955	1	0.672
2011	0.898	0.995	0.888	0.612	0.989	*	0.9	1	*
2012	0.996	0.995	1	0.999	1	1	0.858	1	0.995
2013	0.905	1	0.969	0.883	0.923	0.995	*	0.991	0.972
2014	0.941	0.924	0.997	0.908	0.969	1	*	0.985	0.985

Table 4.3.F: AUROC values for Model 5 for each year (2003 – 2014) and climatic region, * = no data.

Model 5:									
Year/Region:	EA	ES	Mid	NEE	NWENW	SEE	SN	SWESW	WS
2003	0.867	0.961	0.985	0.993	1	1	*	0.987	0.207
2004	0.996	*	1	0.999	0.999	0.995	0.79	0.999	*
2005	0.949	0.971	0.601	0.575	0.931	0.952	*	1	0.925
2006	0.994	0.962	0.919	0.971	0.901	0.974	*	0.973	*
2007	1	0.999	1	1	0.996	0.969	*	1	1
2008	0.938	0.999	0.997	0.999	1	1	*	1	0.999
2009	0.985	1	1	0.996	0.99	1	*	1	0.977
2010	0.972	0.981	1	*	100	0.987	0.994	1	0.913
2011	0.957	1	0.98	0.691	1	*	0.921	1	*
2012	0.999	1	1	0.999	1	1	0.867	1	0.995
2013	0.918	1	0.972	0.883	0.967	0.995	*	0.994	0.972
2014	0.952	0.971	1	0.908	0.989	1	*	0.987	0.997

ANOVA of AUROC values by region and year are provided in Table 4.4. The Smith Period and models 1 and 3 show significant variation in both districts and years, Model 5 don't show significant variation in district or year. Model 2 does not show significant variation in district but shows significance in year.

Table 4.4: Summary ANOVA of AUROC results for the Smith Period and Models 1-5 by region and year

	District		Year	
Model	F (7,72):	P Value:	F(11,72):	P Value:
Smith Period	4.39	<0.001	3.88	<0.001
Model 1	3.89	<0.001	4.19	<0.001
Model 2	1.86	0.088	2.61	0.007
Model 3	3.48	0.003	4.31	<0.001
Model 4	2.53	0.022	2.31	0.017
Model 5	1.82	0.097	1.69	0.093

The low temperature models 1 and 3 did not show significant variation in performance: M1 & M3 = Alert: $F(1, 161) = 0.72$, $p = 0.397$. There was no significant difference between Models 4 and 5, which had both the temperature and relative humidity criteria lowered: M4 & M5 = Alert: $F(1, 161) = 0.72$, $p = 0.397$. Models 1 and 2 did show significant differences in performance: M1 & M2 = Alert: $F(1, 160) = 25.77$, $p<0.001$.

Model 2, defined as two consecutive days each with a minium temperature ≥10°C and at least 6 hours of relative humidity ≥90% was significantly different to the Smith Period and removed the highly signficant variation in performance among found between the climatic districts (Table 4.4 & Figure 4.6). The low temperature models 1 and 3 were a slight improvement on the Smith Period but did not remove the variation among climantic districts. Model 2 showed a larger improvement on the Smith Period and does remove the regional variation in performance but it does not show the high number of alerts seen in models 4 and 5 which have had both their temperature and relative humdity thresholds lowered.

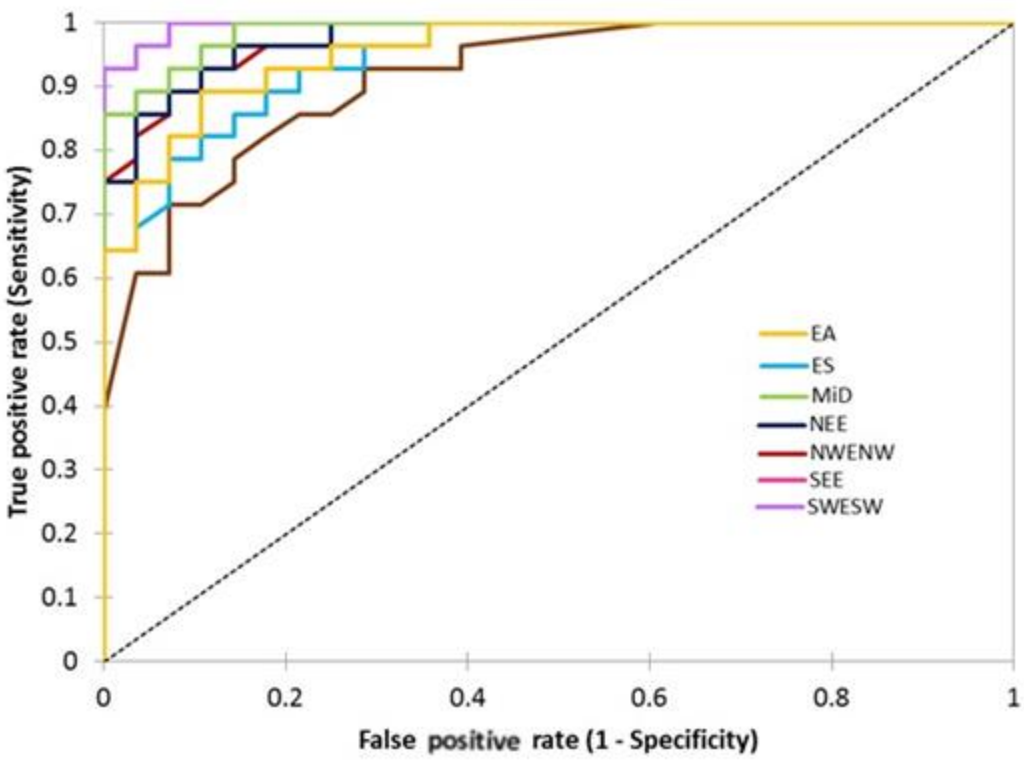

Figure 4.6: ROC Curves for model 2 to determine performance as a diagnostic tool across all climatic districts, including FAB outbreak data from 2003 – 2014.

IDW intepolated heat maps for the number of outbreaks receiving and not receiving alerts 14 and 28 days prior confirm that the Smith Period performed well on coastal regions,with a poorer performance in central regions (Figure 4.8A and 4.9A). This was not the case with model 2, where a more even distribution of outbreaks receiving alerts was evident across the entire country (Figure 4.8B and 4.9 B). This was expected due to the lack of signficance of climatic region in the ANOVA analysis above.

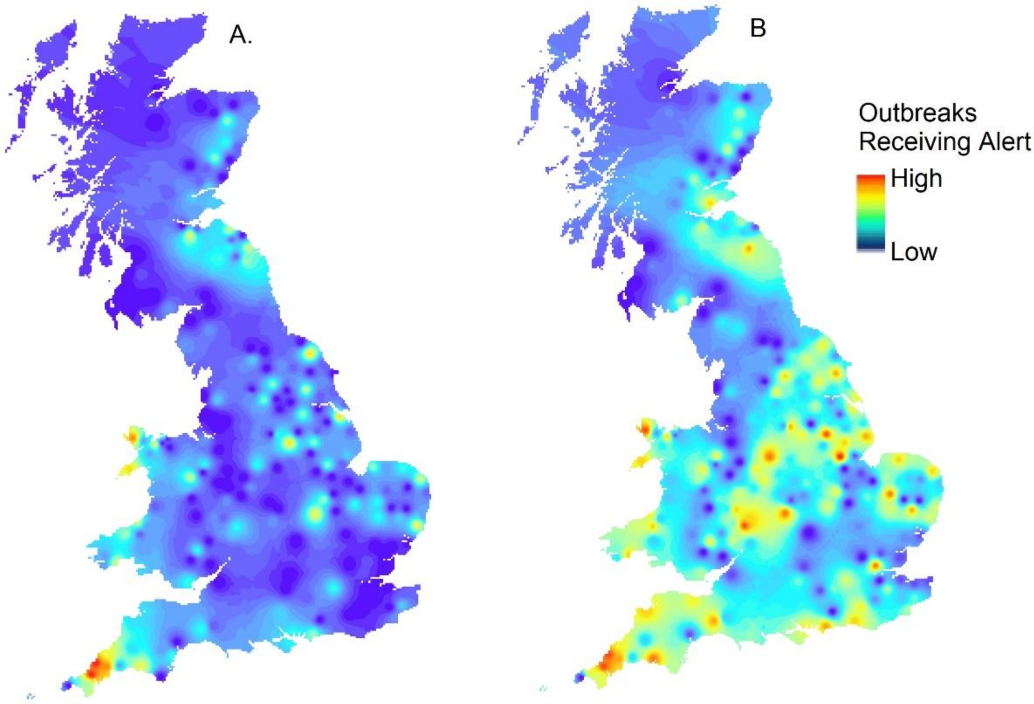

Figure 4.8: Inverse distance weighted maps of the proportion of potato late blight outbreaks from 2003 – 2014 that received (A) a Smith Period, or (B) a model 2 alert in the 14 days prior to the detection of the outbreak.

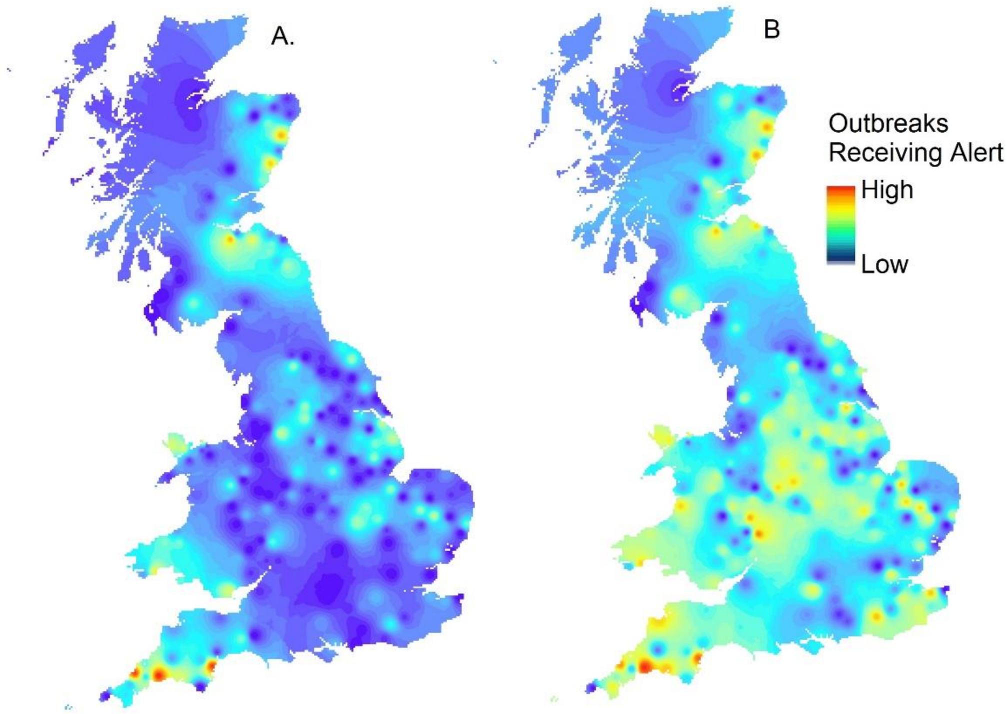

Figure 4.9: Inverse distance weighted maps of the proportions of potato late blight outbreaks from 2003 – 2014 that have received (A) a Smith Period, or (B) a model 2 alert in the 28 days prior to detection of the outbreak.

4.5 DISCUSSION

The results of this study confirm the previous back-testing analysis of the Smith Period (Chapter 2) and the controlled environment experiments on infection in the contemporary pathogen population (Chapter 3), both of which provided evidence that there is a risk of disease development at lower durations of high humidity (≥90% RH) than the 11 hours prescribed by the Smith Period. The candidate replacement model for the Smith Period in which the 10°C minimum temperature threshold was maintained but the duration of high relative humidity required was lowered from 11 to 6 hours (model 2) resulted in a diagnostic tool that was classified as ‘excellent’ according to AUROC values. This was a marked improvement on the Smith Period, which was classified as a ‘fair’ diagnostic tool (Chapter 2). In addition, the low relative humidity duration model had a more uniform distribution of predictive success across GB, as confirmed by an ANOVA of AUROC values (Figure 4.8 B).

The results of the low temperature models that maintained the 11-hour high humidity threshold criterion and reduced the temperature to either 8 or 6°C, were important to test for three reasons; (1) previous experimental research has indicated that current populations of *P. infestans* in GB might be infecting at lower temperatures, (2) growers had expressed that they too felt there was infection below the 10°C threshold, and (3) Syngenta have launched their own set of risk criteria that maintain the 11-hour relative humidity threshold and reduce the minimum temperature requirement to 8°C. In this study the low temperature models produced a slight increase in the number of days receiving an alert, as a threshold criterion had been lowered, but there was only a marginal increase in overall performance compared with the Smith Period, and significant variation in performance across the different climatic districts remained. In the experimental work of Chapter 3 there was a negligible amount of infection below 10°C and those lesions developed very slowly. These results lead us to conclude that reducing the temperature criterion is not required as it will not create a large enough improvement in the system either in overall performance or reducing variation across districts.

Reduction of both temperature and duration of high humidity criteria led to systems that performed very well according to AUROC values (Table 4.3E & F). These models, however, issued many alerts in all years and districts (Table 4.2E & F), indicating that their improvement may not result from being better tailored to the environmental conditions conducive to potato late blight development, but better tailored to the conditions most frequently experienced across Great Britain. Consequently, we do not recommend adoption of these criteria as tools to help with blight management. The 'correct' number of alerts, while considering frequency should be dynamic and reflecting risk and not simply increasing the number of days called overall.

The number of alerts issued by model 2 (16% of days prior to reported outbreaks) was greater than the Smith Period (7% of days prior to reported outbreaks)and the low temperature models (10 and 13% of days prior to reported outbreaks) but unlike models 4 and 5 (24 and 31% of days prior to reported outbreaks) where the number of alerts increased in every year and region, model 2 resulted in a higher number of alerts in years with a large number of outbreaks, and a lower number of alerts in years with reduced disease pressure, the dynamic flexibility in frequency desired by a reliable risk identification system (Table 4.2C).

We therefore conclude that model 2 provides the best prediction outcome; it offers a significant improvement over the Smith Period both in terms of overall predictive accuracy and uniformity of accuracy across GB, and a frequency of alerts of approximately 1 in 7 days. This may sound like a one in seven-day spray schedule, but in reality risk is not received consistently throughout the year. There are periods which are have higher risk frequently – multiple times a week and the identification, especially at the start of the growing season of periods when there is no risk. Model two was renamed the Hutton Criteria and has been launched by AHDB Potatoes as the new national warning system for potato late blight in GB. The Hutton Criteria were integrated into the AHDB Potatoes Blightwatch service and rolled out to the entire GB potato industry at the start of the 2017 growing season. The Hutton Criteria are defined as two consecutive days each with a minimum temperature ≥10°C and at least 6 hours of relative humidity ≥90%. We have confidence in these new criteria due to the confluence of results from the controlled environment experiments and the national-scale longitudinal analyses of late blight outbreak and weather data. The variation in performance across climatic districts was a key factor we wanted to improve upon with a new disease forecasting system, as the potato industry needs system that performs equally for all growers across the country.

The Hutton Criteria are thus a contemporary tool for growers across Great Britain to utilise in the management of potato late blight each year. They occur at a higher frequency than Smith Period alerts, however this is desirable as a lack of alerts was a major criticism of the Smith Period. They are a building block for the further development of DSS's for potato late blight in Great Britain. Additional tools can be developed to work in conjunction with the Hutton Criteria, such as sensors for automated in-field spore detection and process-based models incorporating the development, survival and spread of the pathogen.

5 Chapter Five: Implementation of the Hutton Criteria in 2017 and a brief discussion on weather data and the future of potato late blight decision support tools in Great Britain.

5.1 Abstract

The Hutton Criteria were officially announced in December 2016 as a contemporary risk indicator for potato late blight in Great Britain (GB). The Agricultural and Horticultural Development Board Potatoes (AHDB Potatoes) implemented the Hutton Criteria from 2017 in their national warning system ‘Blight Watch’. The system provided Hutton Criteria alerts throughout the growing season to growers in GB at no cost and based on their postcode district. The performance of the Hutton Criteria in its inaugural year as the national warning system was evaluated using the Fight Against Blight (FAB) recorded outbreaks for 2017 and weather data from a network of in-field AHDB Met stations. Performance was assessed using Receiver operator characteristic (ROC) curves and evaluation of the number of alerts. Feedback from growers was also collected which was positive overall with clarification requested regarding the expected number of alerts each season and whether the relative humidity criteria was to be consecutive or cumulative throughout the day. The AUROC analysis for all regions was >0.9 indicating that the Hutton Criteria was an ‘excellent’ indicator of risk in all climatic districts in 2017. The number of alerts was slightly higher than anticipated from Chapter 4 analysis; however, the Met office showed the year was warmer and wetter than average. Calculation of the relative humidity criteria from cumulative or consecutive periods of high relative humidity did not significantly change the frequency of alerts. The Hutton Criteria overall were a welcomed improvement by growers; a valuable tool in their toolbox for potato crop management.

5.2 INTRODUCTION

The Hutton Criteria are a set of late blight risk criteria, defined as two consecutive days with a minimum temperature of 10°C and at least 6 hours of relative humidity ≥90% on each day. They were developed from a historic analysis of the previous decision support system for late blight in Great Britain, the Smith Period (Chapter 2), controlled environment experiments with contemporary pathogen isolates to identify infection criteria (Chapter 3) and historical testing and validation of alternative risk criteria (Chapter 4). The reason for the Hutton Criteria selection was three-fold:

(1) With an overall area under the receiver operator characteristic curve (AUROC) of [0.973 (95% CI = 0.943 – 1.000)], it was a significantly better diagnostic tool than the previously used Smith Period that had an overall AUROC of [0.686 (95% CI = 0.540-0.832)]

(2) It reduced the significant regional variation found with the Smith Period performance across Great Britain (GB) (Table 4.4).

(3) The number of alerts was greater than the Smith Period, but unlike some of the other alternative models tested, they were not uniformly high across all years and regions but reflected the changing blight pressure from year to year (Table 4.2A-F).

The Hutton Criteria were officially announced in December 2016 and implemented for the 2017 growing season via the Agricultural and Horticultural Development Board Potatoes (AHDB Potatoes) national 'Blight Watch' system (https://blightwatch.co.uk/). Registered users received alerts based on the occurrence of Hutton Criteria in their pre-selected postcode districts. The system is based on met data forecasts for the forthcoming 24 hours. In addition to the AHDB Potatoes system, grower groups have applied the Hutton Criteria within their own local DSS systems and Syngenta included them as an additional set in BliteCast (www.syngenta.co.uk/blightcast).

The Hutton Criteria, after its inaugural year as the national blight forecasting system and the feedback received from the growers throughout the year was evaluated and discussed in this chapter.

5.2.1 Growers Feedback

Feedback was gathered throughout the year by actively seeking out grower's opinions at agricultural events, via articles in the agricultural press and other communication with growers and potato industry contacts such as AHDB Potatoes staff. The Hutton Criteria were reported in multiple media outlets after their launch in December 2016 as, 'an exciting new tool for potato late blight management in GB' (Kellett 2016, Arbuckle 2017, FarmingUK 2016). The published feedback was positive, with several printed interviews with growers reflecting that they appreciated an updated set of risk criteria representative of the pathogen populations currently in the field. Some feedback indicated that the occurrence of Hutton Criteria alerts was greater than anticipated; the occurrence of alerts in 2017 was thus examined. The use of in-field weather stations to calculate localised alerts was evaluated as previously synoptic Met office station data have been used. Alert variations such as calculating the relative humidity criteria consecutively or cumulatively and using one or three hourly average data measurements was investigated to assess variations in alert performance that may be detected by growers running the criteria on their own.

5.3 MATERIALS/METHODS

5.3.1 Data Sets

5.3.1.1 Fight Against Blight Outbreak Data

AHDB Potatoes run the Fight Against Blight (FAB) program, which monitors blight across GB each year with a network of scouts who take samples of blight outbreaks to be genotyped at the James Hutton Institute in Dundee. In 2017 151 FAB outbreaks were recorded and their associated met data was used to assess the Hutton Criteria's performance (Figure 5.1). Outbreaks were subdivided into the climatic districts of Great Britain as has been done in previous analysis (Chapter 2, Chapter 4).

5.3.1.2 Met Data

The AHDB Cereals and Oilseeds network of 63 in-field Met stations covering 38 locations across Great Britain was used to assess the performance of the Hutton Criteria in 2017 (Figure 5.1). The data was provided from the 1st of April to the 6th of October for 2017 and allowed the analysis of 144 of the 151 outbreaks; the other seven outbreaks were reported after the 6th of October. The in-field met station data recorded 15-minute averages of temperature and relative humidity. The Hutton Criteria alerts for the previous historic analysis (Chapter 2 and 4) and for the official 'Blight Watch' alerts were determined from synoptic Met station data from across Great Britain, not in-field data. Unfortunately, data licensing restrictions meant that the 2017 synoptic Met Office data was unavailable for this analysis.

Five in-field sites from Balruddery farm in the DD2 postcode district in Eastern Scotland provided temperature and relative humidity data throughout the 2017 growing season. Two of these locations were 1 meter above the field, two were 2.5 meters above the field and one was a general farm site. The corresponding official Blight Watch alerts for this postcode district were also recorded.

5.3.2 Methods

5.3.2.1 Outbreak and Met station correlation

Each potato late blight outbreak was linked using a nearest neighbour analysis in Arc GIS to the closest AHDB Cereals and Oilseeds in-field Met station.

Calculation of Hutton Criteria Alerts

These met stations were used to calculate Hutton Criteria alerts using the standard format; averaging the hourly data from the 15-minute temperature data to determine the minimum daily temperature and determining the total number of hours of RH ≥90% throughout a 24-hour day. Hutton Criteria alerts occurred if through this the minimum temperature was found to be ≥10°C and there were at least 6 hours with a RH ≥90% for two consecutive days. This analysis also involved investigation into alternative methods of calculating the Hutton Criteria; (1) calculating the relative humidity criteria consecutively throughout the day rather than cumulatively, (2) calculating alerts using Met station data averaged over three-hour periods rather than hourly, (3) calculating one day of Hutton Criteria versus two and finally (4) calculating the previously used Smith Period criteria for further comparison to the previous system.

5.3.2.2 *Receiver Operator Characteristic Curve Analysis*

Receiver operator characteristic (ROC) curve analysis was used to quantify the performance of the Hutton Criteria as a diagnostic tool for indicating high risk periods for potato late blight. This method of analysis was described in Chapter 2.3.2.5. It allows for the assessment of alerts as diagnostic tools to indicate risk prior to known reported outbreaks of disease. The area under the ROC curve (AUROC) is a value from 0 -1 which quantifies overall performance, with values > 0.9 being classed as ‘excellent’ diagnostic tools. ANOVA of AUROC values is a method for comparing resultant curves for various climatic districts of GB and different alert criteria. The analysis was used for the 144 outbreaks in 2017 subdivided by climatic districts, distance of outbreak from AHDB Cereals and Oilseeds Met station and to compare the alternative methods of Hutton Criteria alert calculation and the previously used Smith Period.

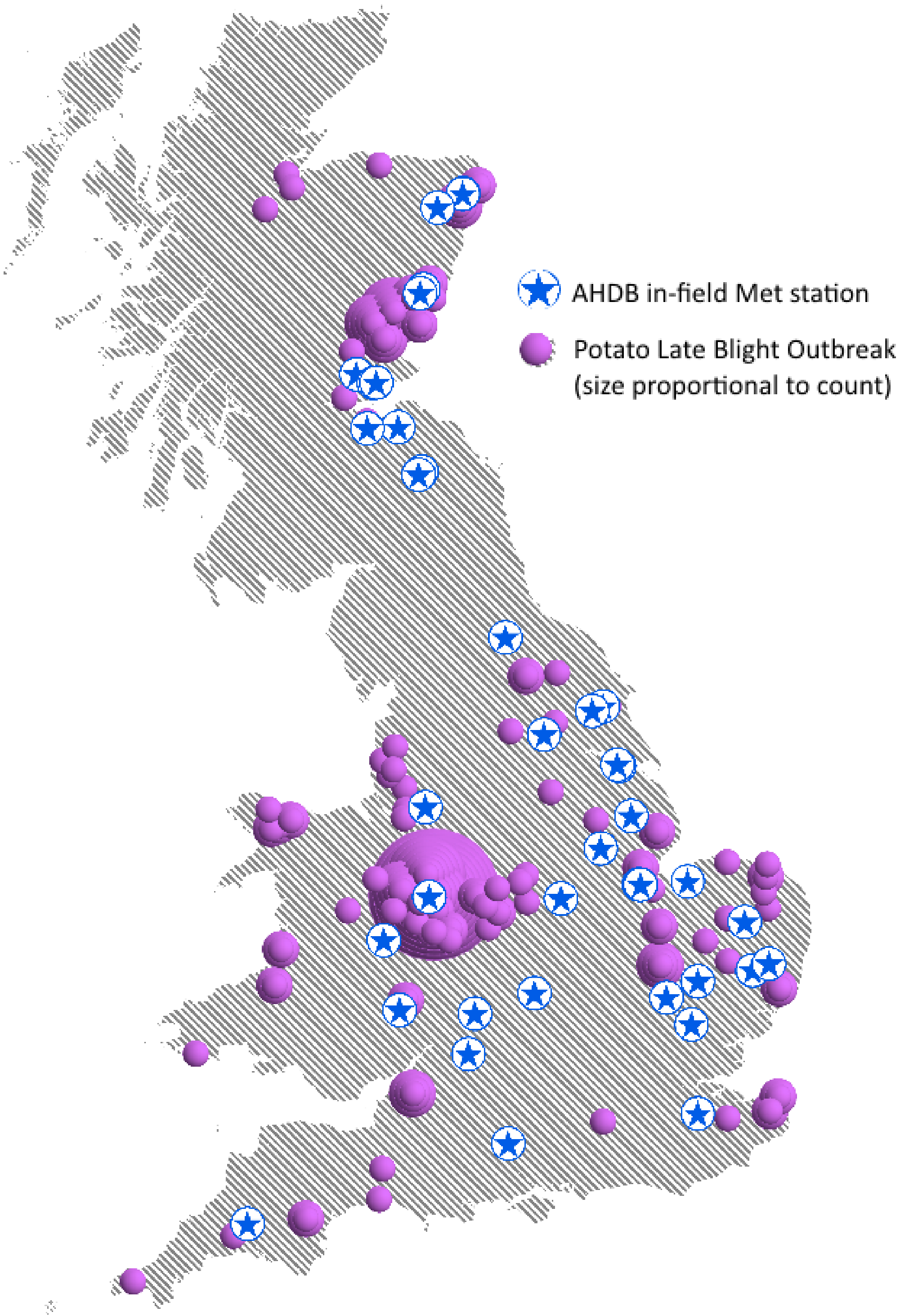

Figure 6.1: Location of recorded FAB potato late blight outbreaks (151) and AHDB Cereals and Oilseeds in-field Met stations across Great Britain in 2017.

5.3.2.3 *Count of Alerts*

The count of alerts throughout the growing season at all AHDB Cereals and Oilseeds Met stations were calculated for Hutton Criteria alerts and the different variations of alert criteria as described above. Alerts were also counted only for days prior to recorded outbreaks at each nearest neighbour linked Met station.

5.4 RESULTS

5.4.1 Outbreak to nearest Met station

Potato late blight outbreaks (144, a reduction of the 151-total number of outbreaks as 7 outbreaks were reported later in the year outside of the window for which we had available Met data) were linked to their closest in-field AHDB Met station. The spread of met stations across the country (Figure 6.1) was not uniform resulting in considerable variation in the distance of outbreaks from their nearest Met station from <5km to >100km (Table 6.1).

Table 6.1: Regional distribution of potato late bight outbreaks in 2017 and distance from nearest AHDB Cereals and Oilseeds in-field Met Station

	Reported FAB outbreaks in 2017 linked to AHDB Cereals and Oilseeds Met stations within:			
	All distances	< 60km	<30km	<15km
Great Britain	144	121	79	39
East Anglia	30	20	13	5
Eastern Scotland	32	29	21	12
Midlands	49	45	36	19
North East England	8	8	5	1
North West England & Northern Wales	14	7	3	1
South East England	12	12	0	0
South East England & Southern Wales	9	9	1	1

5.4.2 Receiver Operator Curve Analysis

ROC curve analysis was performed for all outbreaks across Great Britain and for outbreaks within 60km, 30km and 15km of their closest Met station (Figure 6.4, Table 6.2). Examination of the AUROC curve for all alerts shows that distance of a met station from the outbreak was significant, [F (3, 19) = 3.88, p = .038]. A contrast of the Hutton Criteria with RH calculated cumulatively, and the Smith Period alert shows high significance [F (1,7) = 64.46, p = .004] while a contrast of only the Hutton Criteria alerts with RH calculated cumulatively and consecutively indicates that alert is significant but no longer highly significant [F (1,7) = 11.65, p = .042]. Distance shows the lowest level of significance when only outbreaks within 60, 30 and 15km of the met stations are examined [F (2, 14) = 3.80 p = .069]. When examining distance, the fact that the sample size also decreases with reduced distance must be considered. An area around a Met station will have fewer outbreaks the smaller it is (Table 6.1).

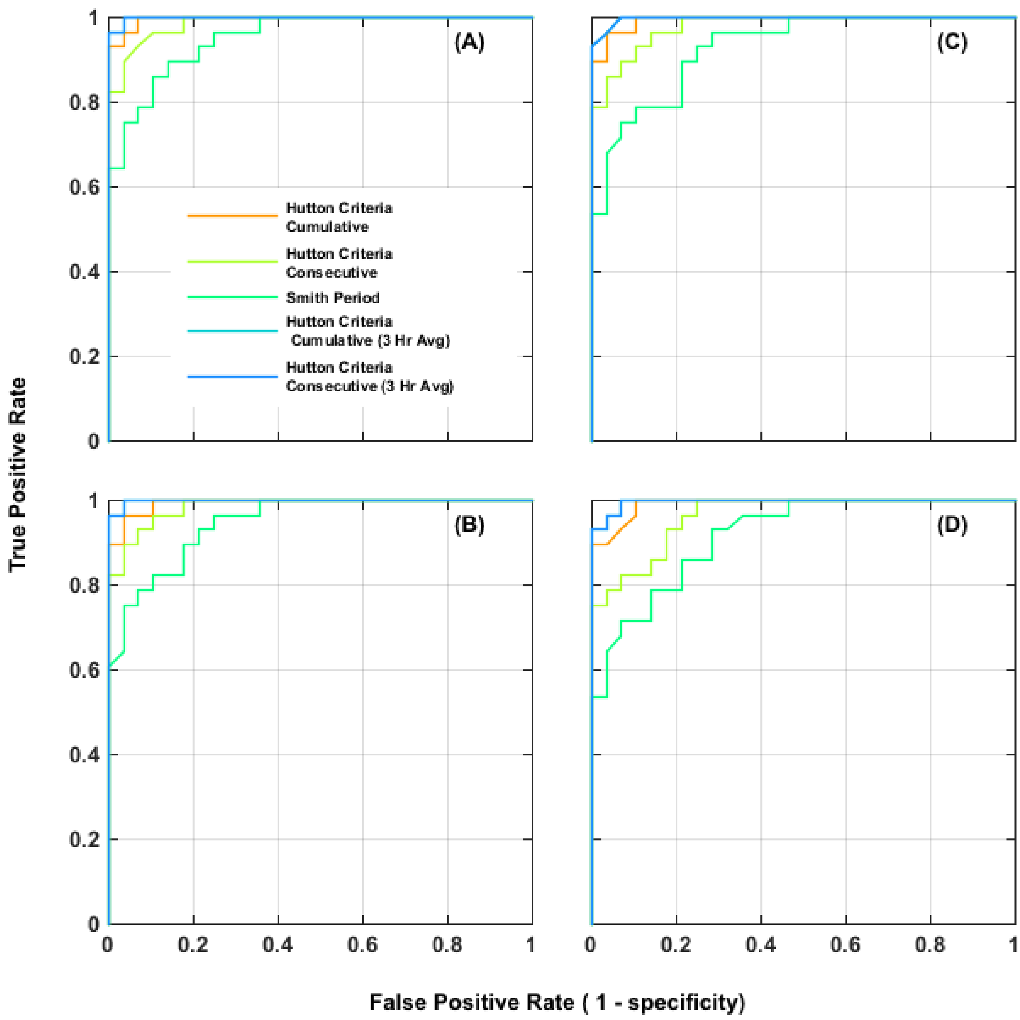

Figure 6.4: ROC curve analysis of potato late bight outbreaks in Great Britain 2017 (A) all outbreaks (B) outbreaks within 60km of the nearest Met station (C) outbreaks within 30km of the nearest Met station and (D) outbreaks within 15 km of the nearest Met station

Table 6.2: AUROC values for 2017 FAB outbreaks grouped based on alert variation and distance from AHDB Met Station

	AUROC for FAB outbreaks within specified distances from AHDB Cereals and Oilseeds Met Station:			
Alert	All	≤60km	≤30km	≤15km
Hutton Criteria (RH Calculated cumulatively)	0.9962	0.9936	0.9936	0.911
Hutton Criteria (RH Calculated consecutively)	0.9859	0.9847	0.9783	0.9617
Hutton Criteria (RH calculated cumulatively, and data averaged over 3 hours)	0.9987	0.9987	0.9974	0.9962
Hutton Criteria (RH calculated consecutively and data averages over 3 hours)	0.9987	0.9987	0.9974	0.9962
Smith Period	0.9515	0.9470	0.9280	0.9171

Further ROC curve analysis into the regional performance of the alerts in 2017 is shown for those outbreaks with a Met station within 60km for Hutton criteria alerts with a cumulative relative humidity, a consecutive relative humidity, a three-hour averaging of met office data and the Smith Period (Figure 6.5, Table 6.3). In the overall AUROC analysis for all results it was found that region was never a significant factor while alert was significant, [F (3, 27) = 4.37, p = .018]. When the Smith Period is removed, and the Hutton Criteria calculated cumulatively, consecutively and using three hourly averaged data is compared alert was no longer considered a significant factor.

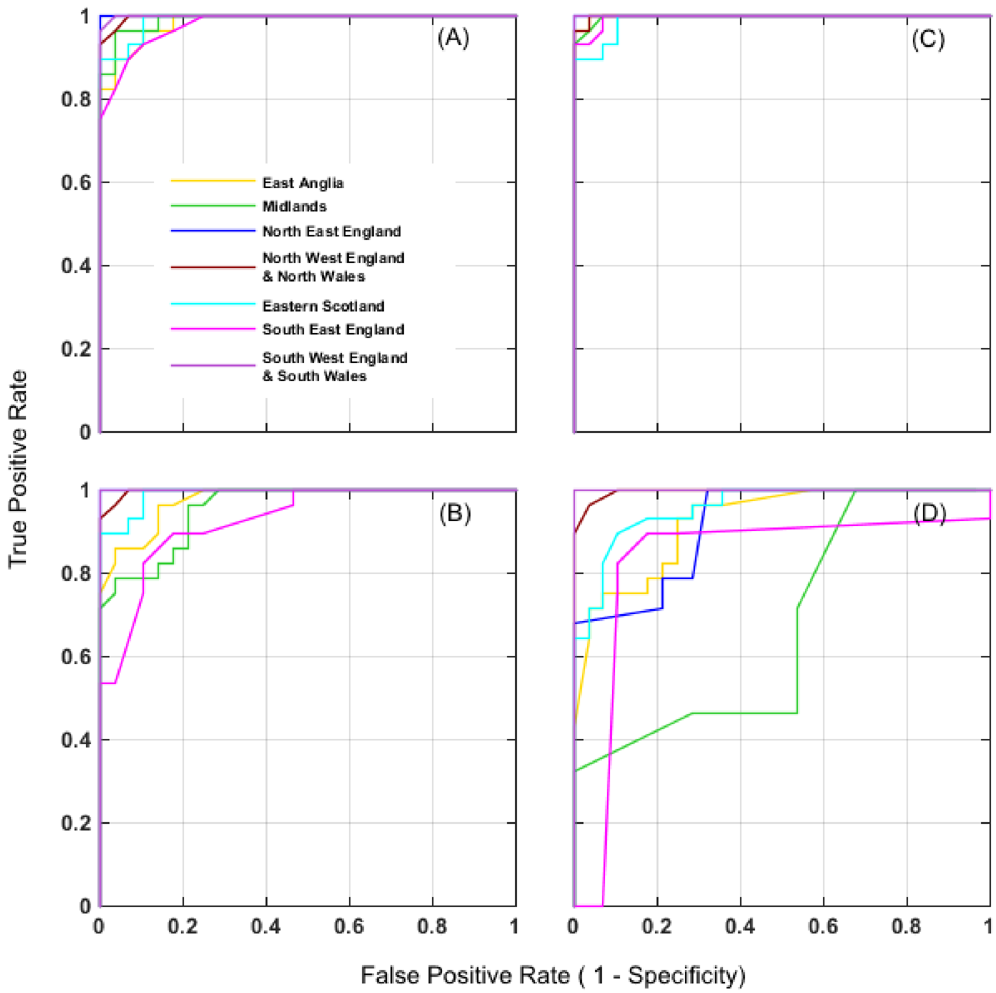

Figure 6.5: ROC curve analysis of potato late blight outbreaks within 60km o their nearest Met station. (A) Hutton Criteria with RH calculated cumulatively (B) Hutton Criteria with the RH calculated consecutively (C) Hutton Criteria with RH calculated cumulatively, and data averaged every three hours (D) Smith Period

Table 6.3: AUROC values for 2017 FAB outbreaks within 60km of their nearest AHDB Cereals and Oilseeds met station, grouped based on alert variation and climatic district

	AUROC for FAB outbreaks within 60km from AHDB Cereals and Oilseeds Met Station:			
Region/Alert:	Hutton Criteria (RH Calculated cumulatively)	Hutton Criteria (RH Calculated consecutively)	Hutton Criteria (RH calculated cumulatively, and data averaged over 3 hours)	Smith Period
East Anglia	0.984	0.9751	0.9987	0.9234
Midlands	0.991	0.9541	0.9974	0.6358
Northeast England	1	1	1	0.9159
Northwest England & Northern Wales	0.9974	0.9974	0.9974	0.9961
Eastern Scotland	0.9898	0.9898	0.9898	0.9554
South East England	0.9789	0.9248	0.9956	0.8219
Southwest England & Southern Wales	0.994	1	1	1

5.4.3 Count of Alerts

The percentage of days receiving alerts was calculated for (1) all days in the growing season and (2) only those days prior to the reported outbreaks, for the entirety of Great Britain but also for each of seven climatic districts where there were reported outbreaks this year; east Anglia, eastern Scotland, Midlands, north east England, northwest England & north Wales, southeast England & south west England & south Wales (Figure 6.2). The number of alerts is always higher when examining the overall growing season (Figure 6.2.A-E) rather than only those days prior to reported outbreaks (Figure 6.2.F-J), as there are more days incorporated into the analysis from the consistently high-risk periods of late July to August for the whole growing season. The Smith Period shows the lowest percentage of days receiving alerts, but it was higher than the averages calculated in the historical analysis (Chapter 2). The number of Hutton Criteria alerts was only slightly lower when calculated with consecutive durations of relative humidity than with cumulative durations. Both alert frequencies increased when calculated using three hourlies rather than hourly average data; this relates to the increased AUROC values seen in Table 6.2 and 6.3.

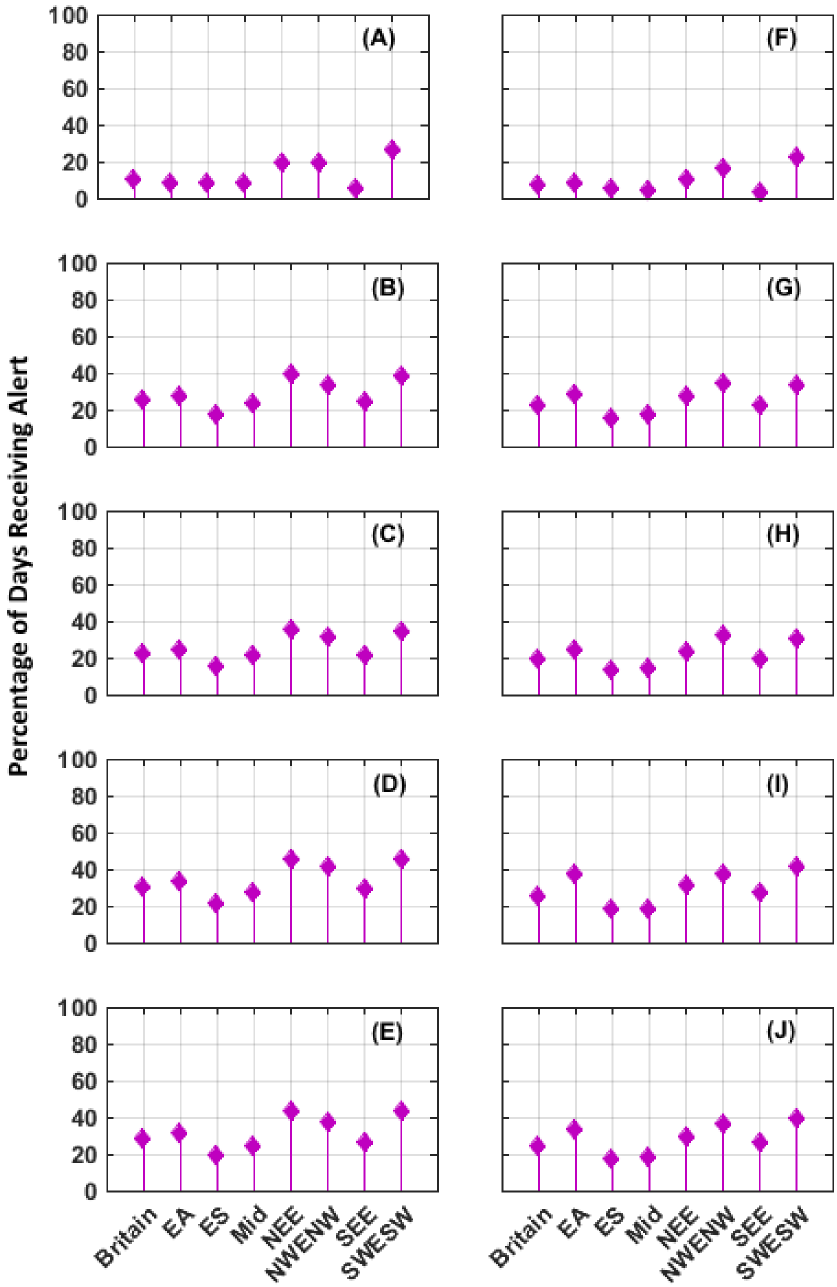

Figure 6.2: Percentage of days receiving alert overall throughout the growing season in 2017, (A) Smith Period, (B) Hutton criteria using hourly averages with RH calculated cumulatively, (C) Hutton Criteria using hourly averages with RH calculated consecutively, (D) Hutton Criteria using three hourly averages with RH calculated cumulatively, (E) Hutton Criteria with three hourly averages and with relative humidity calculated consecutively. Percentage of alerts prior to reported outbreaks in 2017 (1st April – outbreak), (F) Smith Period alerts, (G) Hutton Criteria using hourly averages with RH calculated consecutively, (G) Hutton Criteria using hourly averages and with relative humidity calculated cumulatively, (H) Hutton Criteria using hourly averages with relative humidity calculated consecutively, (I) Hutton Criteria using three hourly averages and with relative humidity calculated cumulatively(J) Hutton Criteria with three hourly averages and with RH calculated consecutively.

Alert frequency at a field site in Balruddery, The James Hutton Institute farm in Eastern Scotland, was examined to study the variation within a single specific location. Alerts calculated by the synoptic Met Office regional network and Blight Watch were compared to those calculated from the Balruddery farm met station and in-field met stations at differing heights in the fields Baruddery CSC and High Pilmore. As expected, there were fewer days with alerts calculated by the Smith Period than the Hutton Criteria in every scenario (Figure 6.3). The proportion of days with a Hutton Criteria did not show any statistically significant variation across the systems and methods of recording met data including Blight Watch, [F (5, 11) = 0.39, p =.839] nor did the Smith Period alerts, excluding Blight Watch, [F (4, 9) = 0.22, p = .914]. In each case, however, it is clear that the fewest alerts came from the regional 'Blight Watch' system compared to on-farm or in-field data. Data recorded with sensors 1m above ground level resulted in a higher proportion of days with alerts than with sensors 2.5m above ground level

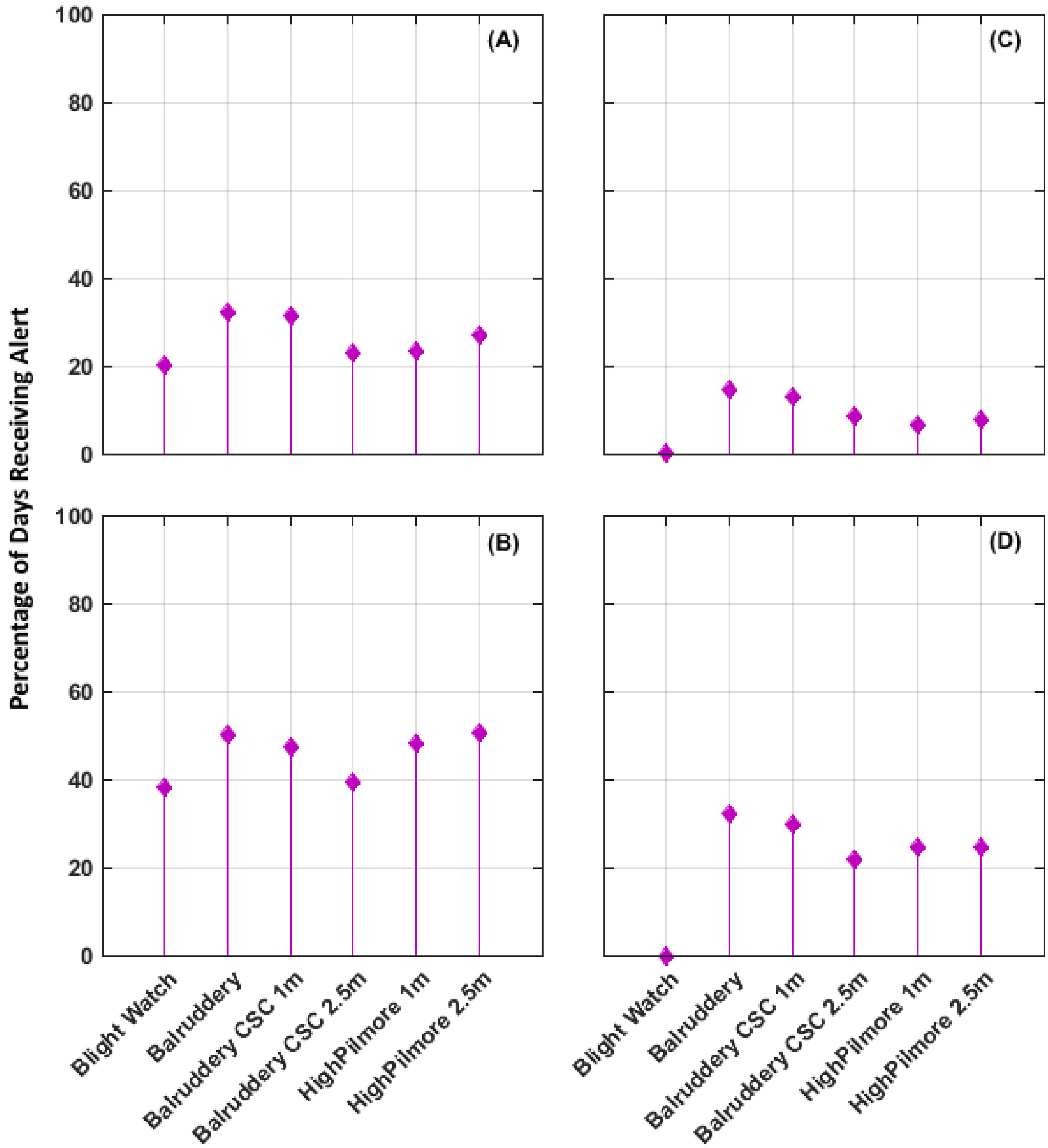

Figure 6.3: A comparison of the percentage of alerts received throughout the 2017 growing season using Blight Watch and multiple different in-field locations and heights for a location in Eastern Scotland for the 2017 growing season. (A) Hutton Criteria, (B) one day of Hutton Criteria, (C)Smith Period (D) one day of Smith Criteria.

5.5 DISCUSSION

Communication with growers and agronomists in 2017 provided real-time feedback of their opinions and concerns regarding the Hutton Criteria. This was extremely important in terms of gauging whether the new decision support tool was of use and value to the key demographic it was aimed at and if there are concerns that needed addressing.

There were many more alerts this year than growers were accustomed to with the previous Smith Period, which may indicate that the new system was overly sensitive. The occurrence of alerts across the different climatic districts were evaluated and it was found that the percentage of days with alerts in 2017 was slightly higher (~24%) than the overall percentage determined from the historic twelve-year analysis (~19%) from which the criteria were developed. It is of note that the twelve-year historic analysis (Chapter 2 and 4) is large enough to accommodate the variation in environmental conditions that can occur from year to year; assessment on any single year will reflect directly the trends of that year's weather. The United Kingdom Met Office (UKMO) freely accessible online weather records showed that the meterological spring in 2017 was warm with a mean temperature of 9.1°C (1.4°C above the 1981 – 2010 average), dry with 192mm of rainfall (81% of the 1981 – 2010 average) and sunny with 498 hours of sunshine (114% of the 1981 – 2010 average). This warm, dry and sunny spring can be related to the slow start in detection of potato late blight outbreaks in 2017; after an initial outbreak detected on the 4th of April there were no further outbreaks detected until the 19th of June. The meteorological summer begins on the 1st of June each year. The summer conditions were much more conducive to late blight, being warm with a mean temperature of 14.7°C (0.4°C above the 1981 – 2010 average), wet with 325mm of rain (135% of the 1981 – 2010 average) and only relatively sunny with 494 hours of sunshine (98% of the 1981 – 2010 averages). The records show that for each month for each climatic region there was a higher than average rainfall showing a sustained increase in moisture throughout the season, which will lead to an increase in risk of potato late blight development. Thus, though the number of alerts in 2017 was slightly higher than predicted using the twelve years of historic data, this relates to the increased risk due to it being a wet and warm year and thus it is appropriate that the number of alerts increases to reflect the increased blight pressure.

Calculation of the relative humidity in the experimental investigations (Chapter 3) examined 6 consecutive hours of relative humidity while our historic analysis (Chapter 4) used cumulative data. It was hypothesized that the natural daily oscillations of temperature and relative humidity lend themselves to high humidity periods occurring consecutively during the first hours of the day. The twelve-year historic analysis (Chapter 4) using the cumulative periods of high humidity showed an acceptable frequency of alerts (19%) and strong performance as an indicator of risk. The Met data received for that analysis was the total numbers of hours each day ≥90%, not specific hourly data. The AHDB Cereals and Oilseeds Met station data was provided in 15-minute averages allowed for more in-depth evaluation. This was important to evaluate as many growers have their own personal in-field Met stations and utilize these to calculate highly localised alerts. This investigation shows the variations that may be seen depending on simple changes made in the calculation of the criteria. The number of alerts increased overall by ~ 2-4 through-out the year when calculated using cumulative versus consecutive relative humidity durations, indicating that most six-hour periods of high humidity are consecutive. This aligned with previous thinking and has been visualized in Figure 6.4 where the oscillations of temperature and relative humidity for a location in Shropshire England for the 16th, 17th and 18th of the months April, May, June, July, August and September are shown. This provides a simple point of reference for the nature of relative humidity and temperature fluctuations every day and highlights the fact that the daily minimums for temperature occur generally at night at the same time as the periods of highest relative humidity. The curve of relative humidity generally oscillates throughout each day with few spikes. Logically if there is a rainy day the relative humidity will be high throughout the day removing the oscillations.

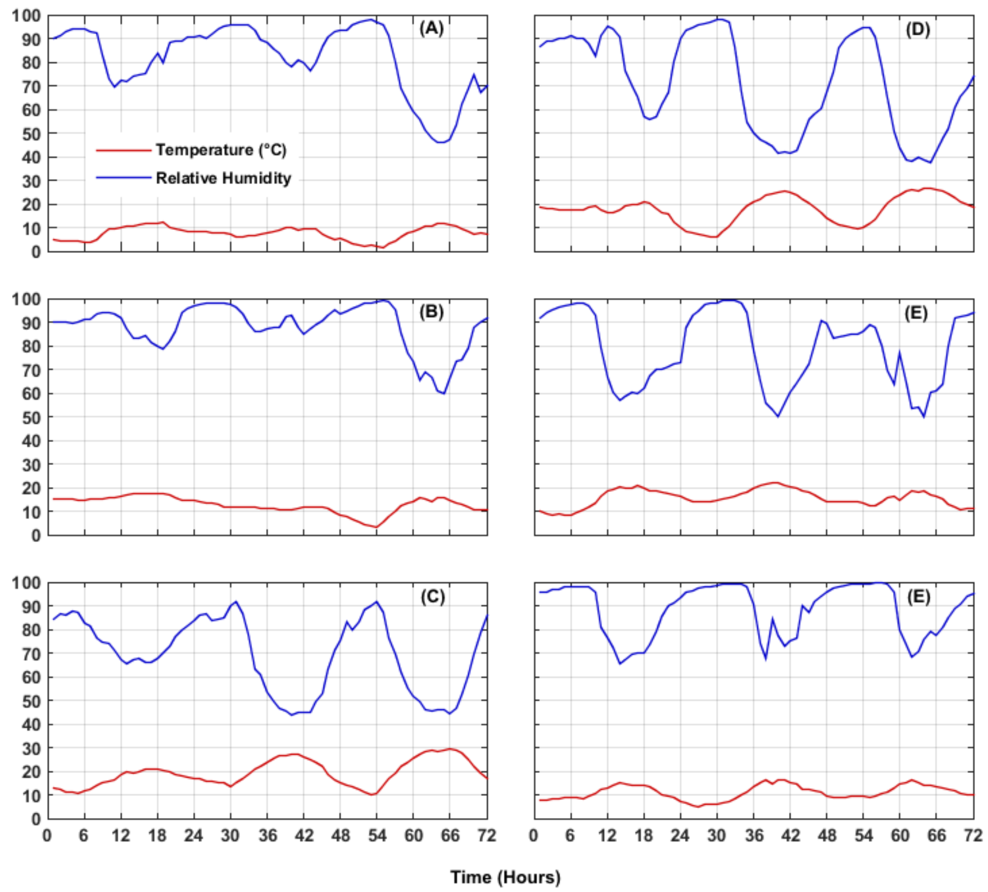

Figure 6.4: Temperature and relative humidity data for AHDB Cereals and Oilseeds in-field Met station in Shropshire for: (A) 16th, 17th & 18th April, (B) 16th, 17th & 18th May, (C) 16th, 17th & 18th June (D) 16th, 17th & 18th July, (E)16th, 17th & 18th August and (F) 16th, 17th and 18th September 2017.

The nature of the Met data provided has a huge influence on the type of analysis preformed and the comparability to future and past analysis. There is a need to identify a uniform structure of Met data to use in the future to ensure that like is being compared with like. The historic data analysis showed benefits in that it provided a uniform spread of data across Great Britain and was the data used to provide the Blight Watch alerts. That provided a measure of confidence in testing the Hutton Criteria. Each interpolated Met station location was further linked to a specific postcode district which would receive an alert, there was no concern regarding distance from outbreak. One could speculate on how related interpolated Met office data from sites such as airfields are to in-field data though.

The AHDB Cereals and Oilseeds dataset provided fifteen-minute measurements which allowed for more detailed evaluation of frequency. There were 38 locations across Great Britain which meant that stations and outbreaks were at a wide range of distances from each other, outbreaks in south west England, north east Scotland and some regions of the south east had Met stations 60 – 100km away. Breaking one year of potato late blight outbreak data down based on region and distance from the Met station does in some cases lead to very small sample sizes which limits the value of the analysis. Thus, the importance of selecting and maintaining a uniform source of Met data is integral for development and maintenance of any decision support system, only with an agreed standardized structure of data can useful comparisons be made to build even more robust systems for disease management in the future.

The use of highly localised in-field Met data is increasing with growers. We thus utilized a local area of Eastern Scotland to examine the effect of in-field data in direct comparison with the official Blight Watch alerts. While our historical analysis was performed using Blight Watch alerts the evaluation in 2017 was performed using in-field data, we did not have overlapping data for either year to compare. Though the frequency was higher than expected in 2017 this was attributed to the Met Office seasonal data indicating that it was a warmer and wetter year than average across the country. Perhaps though too this could be related to the use of in field data compared with the interpolated Met office data for which the system was designed. The results from the case study in Eastern Scotland showed that, every in-field station had a higher frequency of alerts than Blight Watch. The Balruddery CSC station shows that the number of alerts can increase the closer you get to the field, showing more alerts at the same location at 1m above the field than 2.5m. This was not surprising, knowing that the microclimate in any field will be different to that recorded on standardised Met Office stations.

It is known that the frequency of Hutton Criteria alerts based on in-field data will be higher than that expected from Blight Watch. It is predicted that the Blight Watch Hutton Criteria are an excellent indicator of high risk conditions for blight development (Chapter 4). If in-field met data increases the sensitivity of the alert system, then this is indicative of the disease pressure that growers face every year in managing potato late blight and justifies the heavy reliance on a regimented fungicide spray programme. Knowing that the Hutton Criteria is a highly sensitive measure of risk will perhaps provide growers with greater confidence when a fungicide spray is not required. Providing growers with an accurate measure of when they should start their fungicide programme at the beginning of each growing season and when less effective (and thus less expensive) products may be used within the spray programme.

This discussion leads us to the future of decision support systems for potato late blight in Great Britain. This study provides confidence that the Hutton Criteria provides an accurate indication of high risk conditions and an excellent foundation for blight management in GB. It assumes that *P. infestans* sporangia are ever-present and viable. The future of potato late blight management will come from greater knowledge of in-field conditions regarding the presence of the pathogen and disease. Specifically, the use of in-field spore traps for detection of *P. infestans* (Harrison, Livingston & Oshima, 1965, Ronneberger, Burkhardt & Schultz, 2002). A network of such spore traps established across Great Britain to aid growers in accurately tailoring spray schedules and reduce the number of fungicide sprays offers both environmental and economic benefits.

A deeper understanding of the first outbreak analysis each year and disease development based on factors such as inoculum hotspots, disease build up in previous years, geographic patterns of spread based with topography, wind and other environmental factors will be modelled in coming years. The FAB outbreak data set from 2003 – 2017 is an immensely rich resource to mine to understand the patterns of disease movement, development and spread across Great Britain. Genotypes such as 6_A1 and 13_A2 have been recorded since their first appearances in Great Britain by FAB and the story of their rise, spread and dominance in the Great British populations will be a very interesting tale to unravel which will be able to provide an example from which to base our future management of new genotypes such as 37_A2 which appeared in Shropshire in 2016 and showed resistance to fluazinam (Schepers, 2017). Existing studies at the James Hutton Institute aim to develop a new set of tools for growers to add to the Hutton Criteria and their integrated pest management toolbox, creating more confidence in disease management for the future. A set of tools that not only indicates risk, but patterns of disease spread, in-field detection and sporangial survival in the face of adverse conditions will aid disease management. The Hutton Criteria is an integral first step in a modern DSS for blight management in Great Britain, using the sophisticated research methods and reflecting the pathogen genotypes currently present in the field.

6 CONCLUSIONS

The Hutton Criteria are the new national warning criteria used in Great Britain to indicate periods of risk for potato late blight in the field. They have been used in the Agricultural and Horticultural Development Board Potatoes (AHDB Potatoes) ‘Blight Watch’ system since 2017. This a free to use system for growers across the country to access information based on their post code district of when risk criteria have occurred using one day forecasted data, as well as providing the opportunity for the grower to look back retrospectively at temperature and relative humidity data.

There are a wide variety of decision support systems (DSSs) available for potato late blight with a range of complexities, from simple risk criteria (Bourke, 1955, Førsund, 1983), to those providing fungicide spray advice (Fry, Apple & Bruhn, 1983) or those providing information on the spatial spread of sporangia (Hadders, 2008). The Hutton Criteria are a simple set of temperature and relative humidity risk criteria, two consecutive days where on each day the minimum temperature is ≥10°C and there are at least 6 hours of relative humidity ≥90%, indicating that environmental conditions in the field are conducive for *P. infestans* infection. The occurrence of these criteria in a grower’s post code district indicates that they should adjust their fungicide spray and crop management to deal with the threat. Conversely the absence of these criteria indicates that risk is low. DSSs for risk often use an accumulation factor with risk, which allows for risk to be calculated across a wide range of temperatures and relative humidities, different combinations for different durations creating different magnitudes of risk (Ullrich & Schrödter, 1966, Nugteren, 1996, Hadders 2008). The Blight Watch website allows growers to see if multiple Hutton Criteria have occurred in quick succession of each other though and a grower intuitively understands this to create a greater risk. The use of complex or simple DSSs have both positive and negative aspects, a simple DSS, such as the Hutton Criteria can easily be utilized by growers with their own meteorological equipment and easily provided free of charge across all of Great Britain, providing all growers with free information to help improve their crop management.

The Smith Period, the risk criteria in use prior to the Hutton Criteria, were established in the 1950’s and had not been assessed in over 60 years, prior to this investigation. The Smith period was previously used in the Blight Watch system and was well known to growers and industry in GB; two consecutive days with a minimum temperature of 10°C and at least 11 hours ≥90%RH. It was widely accepted that temperature and relative humidity were crucial factors for indicating risk, there was speculation about whether the Smith Period had the correct thresholds of these criteria it was suspected that contemporary strains of *P. infestans* infected below the 10°C temperature threshold.

Investigations of the Smith Period performance using a data set of >2000 historical potato late blight outbreaks recorded across GB through the ‘Fight Against Blight ‘campaign from 2003 -2014 and corresponding synoptic United Kingdom Met Office (UKMO) data showed that ~20% of outbreaks in each climatic district of the country were not receiving Smith Period alerts in the previous 28 days prior to outbreaks. Receiver operator characteristic (ROC) curve analysis further identified the Smith Period as a ‘fair’ diagnostic tool and showed that there was significant variation in performance across the different climatic districts of Great Britain.

The changing populations of *P.infestans* in GB were suspected to be fitter and able to infect outside the Smith Period criteria (Cooke et al., 2012 , Chapman 2012), the ideas of which drove experimental investigation using contemporary isolates of *P. infestans* to quantify the infection criteria of the modern populations. Controlled environment experiments utilized glycerol-water solutions to investigate relative humidity levels in chambers placed within controlled temperature environments. The minimum relative humidity threshold of 90% was found to be suitable as there was negligible infection at lower relative humidity levels. Interestingly the infection rate below the 10°C threshold of the Smith Period was found to be very low as was the lesion growth rate of infection that did occur, which does not indicate that a lower temperature threshold would lead to an improved criterion for identification of risk. Whole plant experiments which investigate duration of high relative humidity exposure found that exposure to shorter durations of high relative humidity 6 hours versus the 11 hours of the Smith Period saw a reduction in infection efficiency of only ~11%, indicating that a simple modification to the Smith period, a DSS which growers and industry across Great Britain were already familiar with, may lead to significant improvements in identification of high risk conditions for blight development.

The historic FAB outbreak data, 2003 – 2014, with corresponding UKMO data was used to test alternative risk algorithms and compare the results with the Smith Period. Low temperature models were tested as the conviction was strong amongst many growers and the industry that the temperature threshold criteria, if modified would see significant improvements. Lowering the temperature threshold to both 8 and 6°C improved the performance of the criteria slightly, but it was not a large enough increase to warrant changing the whole system, indeed the improved performance seemed related simply to a larger number of days being called, there was no change in performance across the different climatic districts of the country. Maintaining the minimum temperature threshold of 10°C and reducing the duration of high relative humidity exposure from 11 hours to 6 hours, directed by experimental findings, showed a significant increase in performance across GB and removed the regional variation in performance. The alerts were more frequent; however, their increased frequency could be related to ‘bad blight years’ and not an equal increase across all years in all conditions, indicating that the increase in alerts relates to increased blight pressure.

This model was selected, as the Hutton criteria and launched in December 2016 and used nationally in the Blight Watch warning systems during the 2017 growing season. The results of the inaugural year indicated that it did indicate high risk periods for late blight development. The risk was high in 2017 from mid-June as it was warmer and wetter than average, this meant that there was a lot of blight pressure and a high number of alerts, so much so that the Smith Period performed well in 2017 as well, which it was known to do in some high-pressure years such as 2012. The increase in Hutton Criteria alerts was ~5% more days than the twelve-year historic analysis predicted would receive alerts. This is an acceptable fluctuation considering that there was increased risk.

The system will continue to be monitored in 2018 and subsequent years, with more knowledge of performance coming from a greater number of years implemented and more feedback from growers. The simple modification to the existing Smith Period, which we know through experimental and historical analysis improves the system, is easy for growers across the country to adopt and for the Blight Watch system to implement. The use of a completely new DSS would have a longer teething period and take longer for growers to place confidence in. There is consensus that temperature, relative humidity and duration of exposure are conducive to risk from potato late blight. Selecting the right combination of these criteria to show sensitivity and specificity as an alert system is integral. Establishment of a simple DSS which has been scientifically evidenced to indicate high risk criteria in-field for contemporary genotypes of *P. infestans* creates a foundation stone from which more advanced DSS elements can be built.

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